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SOME OPINIONS OF THE PRESS.

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Glasgow Herald.

TEXT-BOOK
OF THE
EMBRYOLOGY OF INVERTEBRATES

TEXT-BOOK

OF THE

EMBRYOLOGY OF INVERTEBRATES

BY

DR. E. KORSCHELT,
PROFESSOR OF ZOOLOGY AND COMPARATIVE ANATOMY IN THE UNIVERSITY OF MARBURG.

DR. K. HEIDER,
PROFESSOR OF ZOOLOGY IN THE UNIVERSITY OF BERLIN.

TRANSLATED FROM THE GERMAN
BY
MATILDA BERNARD.

REVISED AND EDITED WITH ADDITIONAL NOTES
BY
MARTIN F. WOODWARD,
DEMONSTRATOR OF ZOOLOGY, ROYAL COLLEGE OF SCIENCE, LONDON.

VOL. III.

ARACHNIDA, PENTASTOMIDAE, PANTOPODA, TARDIGRADA, ONYCHOPHORA, MYRIOPODA, INSECTA.

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PREFACE.

The present and third instalment of the translation of the *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere* contains the Arachnida and appended groups, the Onychophora, the Myriopoda, and the Insecta, thus completing the Arthropodan portion of this work. The remaining volume, which contains the Mollusca, Ascidia, and Cephalochorda, will, I hope, be published at the end of the year.

In connection with the present volume, I have to thank Mr. R. I. Pocock for his valuable assistance in the Arachnidan part, and also I have to thank Mr. A. D. Michael, who kindly read through the chapter on the Acarini and corrected many errors in the same. Most of the suggestions made by these gentlemen have been added as editorial footnotes, but some matter, when the original was obviously at fault, has been placed in the text.

The very important work by Brauer on the Ontogeny of the Scorpion renders some of the text relating to this genus out of date, and this work should certainly be consulted by those studying the Arachnida. His discovery of an additional segment between the thorax and abdomen is of especial importance in the interpretation of the Arachnidan body. In this connection it is interesting to note that this segment was correctly figured, though misinterpreted, by Metschnikoff in 1871, as a careful comparison of the figures of these two authors will show.

In the Onychophora, Willey's paper on *Peripatus novae-britanniae* is of great importance, especially in connection with the invagination germ-band in the Insecta and the interpretation of the embryonic membranes.

Among the numerous additions to the literature on the Insecta, Heymon's works, especially that on *Lepisma*, are worthy of careful study. Unfortunately, the interpretation of the ontogenetic processes in the Insecta is very difficult, and in consequence we still find a terrible confusion enshrouding the origin of some organs, especially that of the alimentary canal, which a number of recent authors maintain to be entirely ectodermal, a condition which, judging from what occurs in other Arthropods, seems extremely improbable.

The germ-cells, as in the two previous volumes, are still treated of as mesodermal, whereas, as has been pointed out in the editorial notes to Vols. i. and ii., these cells are probably handed down from parent to offspring as distinct and continuous structures, their identity being temporarily merged in the egg.

In the present volume I have added more notes and literature and made more alterations in the text than in Vol. ii., and I hope that such alterations will tend to bring this volume more up to date.

MARTIN F. WOODWARD.

ROYAL COLLEGE OF SCIENCE, LONDON.
July, 1899.

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CHAPTER XXI.

ARACHNIDA.

Systematic:—

I. Scorpiones.
II. Pedipalpi.
III. Palpigradi (Koenenia).
IV. Pseudoscorpiones.
V. Opiliones.
VI. Solifugae.
VII. Araneae.
VIII. Acarina.

I. Scorpiones.

The Scorpiones are viviparous. The oval or spherical eggs, which are rich in yolk and are each surrounded by a thin membrane, lie in follicles that arise as outgrowths of the walls of the ovarian tubes. Fertilisation takes place either in the ovarian follicles (*Euscorpius* and *Scorpio*, Metschnikoff, Laurie), or when the egg has left the follicle and passed into the ovarian tube (*Androctonus*, Kowalevsky and Schulgin). In the former case the embryo remains in the follicle during the greater part of its development (*Scorpio*, Joh. Müller), or leaves it when the formation of the germ-band commences (*Euscorpius italicus*). Further development then takes place in the ovarian tubes or oviducts, which thus function as uteri. At birth the young resemble the adult in their general organisation.

1. Cleavage and Formation of the Germ-layer.

The cleavage of the egg in Scorpions is discoidal. At the pole of the egg, which is directed from the follicle towards the ovarian tube, in the youngest stage as yet observed, there were found a number of cells which formed a small unilaminar cap on the yolk; this is the germ-disc (Fig. 1). The blastoderm spreads gradually from this point, advancing very slowly over the yolk (Fig. 2 *A* and *B*). Long before it has grown round the latter, however, the rudiment of the germ-band has appeared, and the first differentiation of the latter takes place at the point where the blastoderm first began to form. A cleavage of the yolk, such as is met with in the eggs of the Araneae, does not occur in the Scorpiones.

The discoidal cleavage of the Scorpiones might be compared with the Crustacean method of cleavage distinguished as Type IV., and might, like the latter, be traced back to superficial cleavage (Vol. ii., pp. 117 and 118). This would be the more permissible as superficial cleavage is, as a rule, widespread among the Arachnida also. In this respect the Scorpiones, as compared with the Araneae, must be considered as showing a modified condition, although they are in other respects more primitive. The development of the embryo within the body of the mother is a sufficient proof that modification in the primitive method of development has taken place.

The Formation of the Germ-layers. The germ-disc does not long retain the character of a single layer of cells. A thickening appears at its centre, which, on the surface turned towards the yolk, appears as a swelling. This, according to KOWALEVSKY and SCHULGIN, has arisen by a down-sinking of the cells. If we bear in mind, in addition to this, the longitudinal furrow described by METSCHNIKOFF on the surface of the now oval germ-disc (Fig. 4 *A*, p. 6), we are reminded of the long slit-like blastopore that occurs in *Peripatus* and in the Insecta, and which constitutes the longitudinal germinal groove. In any case, the differentiation of the inner and middle germ-layers starts from this point.

FIG. 1.—Egg of *Euscorpius italicus* showing the germ-disc (after METSCHNIKOFF, from BALFOUR's *Text-book*).

LAURIE (No. 23), in his recent work, does not actually deny the "down-sinking" of the cells and the presence of the longitudinal furrow, but being unable to convince himself, seems inclined to doubt their existence. This, indeed, cannot be considered as established, especially as the descriptions given of these processes are not very exact. LAURIE derives the ento-mesoderm by delamination from the cell-mass of the germ-disc, in which no special regularity of structure is apparent. But he also finds a thickened point at the posterior end of the germ-disc, in which rapid increase of cells takes place (formation of the ento-mesoderm), and which could therefore be compared with an invagination (Fig. 3, *A, e*). The caudal prominence described by METSCHNIKOFF (No. 24) is probably to be identified with this growing point; the former projects into the yolk, and at a later period shifts into the caudal region of the embryo. LAURIE compares the thickened part with the primitive streak in vertebrates, and we are again involuntarily reminded of the conditions found in *Peripatus*. In the latter the "point of ingrowth" lies at the posterior end of the long blastopore.*

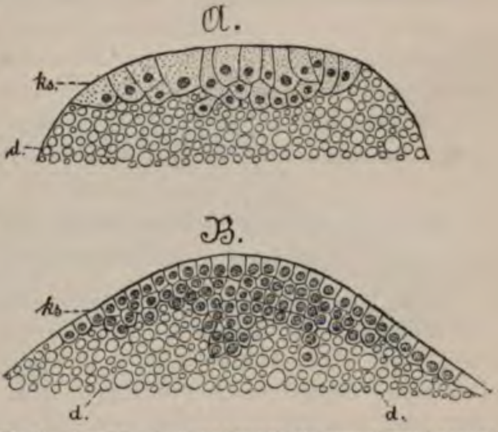

FIG. 2.—*A* and *B*. Sections through the germ-disc and part of the yolk of *Euscorpius italicus* (after LAURIE). *d*, yolk; *ks*, germ-disc.

When the germ-disc, by the active increase of its elements, has attained a thickness of several cells, these still appear but slightly differentiated into layers. The inner surface of the germ-disc is now quite irregular, for single cells become detached from it, and shift into the yolk (Fig. 2, *B*). These cells give rise to the amoeboid yolk-cells, which are distributed throughout the yolk, and bring about its disintegration, *without, however, taking part in the formation of the embryo* (KOWALEVSKY and SCHULGIN, LAURIE, [BRAUER]). They thus differ from the corresponding cells in the Araneae, which participate in the formation of the enteron. The entoderm of the Scorpiones arises by the differentiation of the cells of the germ-disc lying next to the yolk to form a regular epithelium (Fig. 3, *A* and *B*, *ent.*). The cells of this layer differ further from the adjacent cells by their highly-refractive appearance, due to the fluid yolk which they have absorbed.

The mass of cells which, after the differentiation of the entoderm, remains between it and the ectoderm, corresponds to the mesoderm

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* [BRAUER (App. to Lit. on Scorpiones, No. II.), in his interpretation of this posterior thickening of the blastoderm, disagrees with all former investigators; he sees in this thickening the genital rudiment. The mesoderm-cells arise in front and at the sides of this thickened area as proliferations from the ectoderm. The entoderm arises by delamination from the primary blastoderm, and is first observed between the yolk-cells on the one hand, and the ectoderm or the genital rudiment on the other.—ED.]

(Fig. 3, *A* and *B*). At first this is an irregular mass, extending over the whole region of the germ-disc, but at a later stage it takes the form of two symmetrically arranged bands situated near the middle line. These two bands, which fuse with one another posteriorly, become divided up later into the primitive mesodermal segments, each of which contains a cavity (Fig. 3, *B*, *mes*).

The increase in amount of the mesoderm is due to a multiplication of the cells of the primitive entoderm from which, in places, it is not yet differentiated (LAURIE). If it were the case that the principal increase of the cells proceeded from a point at the posterior end of the germ-disc, a growth of the mesoderm-bands from behind forward would result, such as is found in many other segmented animals. The differentiation of the mesoderm-bands would then proceed here, as in those forms, from before backward.

2. The Origin of the Embryonic Membranes and the Development of the External Form of the Body.

During the processes just described, the germ-disc has extended but little over the yolk, and still appears as a rounded, or somewhat oval, disc. Even at this early stage the formation of *embryonic membranes* begins. A groove appears near the periphery of the germ-disc, running right round it and marking off the central portion of the disc in the form of a slight prominence rising from the narrow peripheral area. At the edge of the groove a fold of the ectoderm rises, and this now grows from the periphery over the germ-disc, finally fusing at its centre. The two lamellae of the embryonic envelope are thus formed. The outer membrane, which lies immediately below the egg-integument, is the *serosa*, and the inner, the *amnion*. During the formation of this ectodermal fold a few mesoderm cells are said to pass in between its two lamellae (KOWALEVSKY and SCHULGIN).

According to KOWALEVSKY and SCHULGIN, the formation of the embryonic envelopes in the Scorpiones (at least in *Androctonus*) takes place in the same way as in the Insecta and Vertebrata. LAURIE, who investigated *Euscorpius italicus*, came to a different conclusion regarding the origin of these membranes, he thought that the two cell-layers which form the serosa and the amnion grow independently over the germ-disc from its periphery. The serosa appears first as a layer of cells which rises all round the edge of the germ-disc, and grows towards the centre, where it fuses. Only after this fusion does a second layer, the amnion, appear, and pass through the same process (Fig. 3, *A* and *B*). Such an outgrowth of a single layer of cells is difficult to understand, and must no doubt have originated as a fold of ectoderm consisting of two layers of cells.

The method observed by Kowalevsky and Schulgin must, therefore, be regarded as the more primitive. Somewhat similar processes are, also, to be found in the Insecta (especially in the Hymenoptera), in which the outer layer of the fold grows out beyond the inner, leaving the latter behind, so that it appears vestigial or else altogether disappears (*cf.* the account of these processes which is given below in connection with the Hymenoptera, the *Aphidae* and *Oecanthus*). In such cases the embryonic envelope consists solely of the outer membrane, the serosa. Reduction does not, apparently, go as far as this in the Scorpiones, two membranes being always found in them (Metschnikoff, Ganin,* Blochmann). Metschnikoff also found that the amnion forms later than the serosa, and this seems to confirm Laurie's view, although

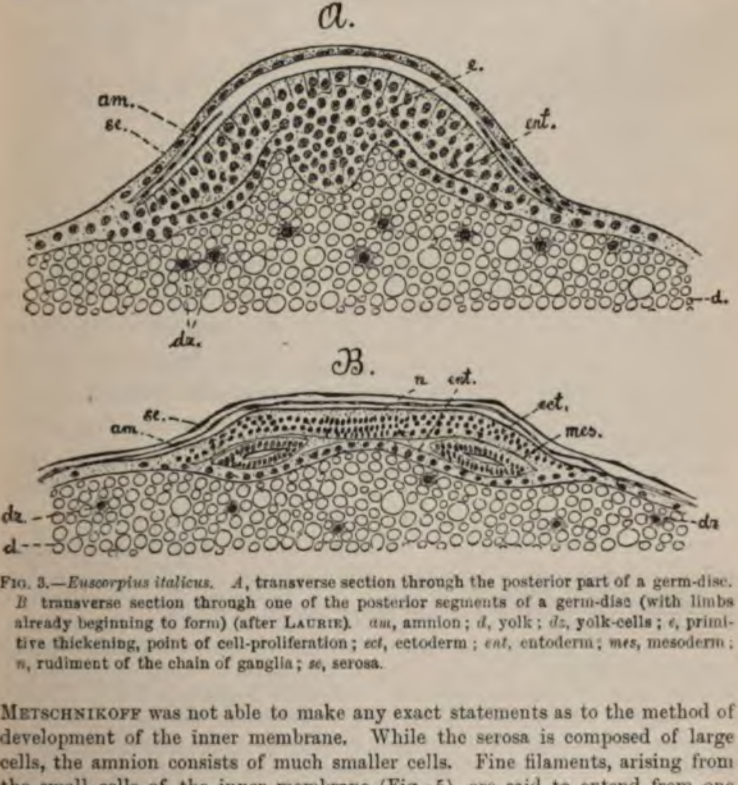

Fig. 3.—*Euscorpius italicus.* *A*, transverse section through the posterior part of a germ-disc. *B* transverse section through one of the posterior segments of a germ-disc (with limbs already beginning to form) (after Laurie). *am*, amnion; *d*, yolk; *dz*, yolk-cells; *e*, primitive thickening, point of cell-proliferation; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm; *n*, rudiment of the chain of ganglia; *se*, serosa.

Metschnikoff was not able to make any exact statements as to the method of development of the inner membrane. While the serosa is composed of large cells, the amnion consists of much smaller cells. Fine filaments, arising from the small cells of the inner membrane (Fig. 5), are said to extend from one membrane to the other.

The mesoderm cells which, according to Kowalevsky and Schulgin, extend between the two membranes of the embryonic envelope, recall the particles of yolk which occasionally occur between the amnion and the serosa in the Insecta, a phenomenon which is explained by the method of origin of these

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* Ganin's Russian treatise on the ontogeny of the Scorpion (No. 18, 1867), which, as far as we know, is not illustrated, we were not able to examine.

envelopes. Laurie discovered no mesoderm-cells between the embryonic integuments. It will only be possible to form a reliable opinion on this subject after the appearance of Kowalevsky and Schulgin's complete work; as yet we have only a preliminary sketch unaccompanied by figures (No. 19).*

During the formation of the germ-layers and the development of the embryonic envelopes the germ-disc changes its shape, becoming broader at its anterior end (Fig. 4 *A*). The narrow posterior part becomes greatly thickened through active proliferation of cells. In the middle line there appears on the surface of the disc the groove-like depression already mentioned, which soon disappears again (Fig. 4 *A*, after Metschnikoff). The cephalic region becomes marked off from the primary trunk-region by a transverse furrow near the anterior end of the germ-disc, and about the same time, or very soon after, a few transverse furrows appear further back, these being the rudiments of the first body-segments and of a large posterior region. This is followed by the separation of further segments from this latter region (Laurie).

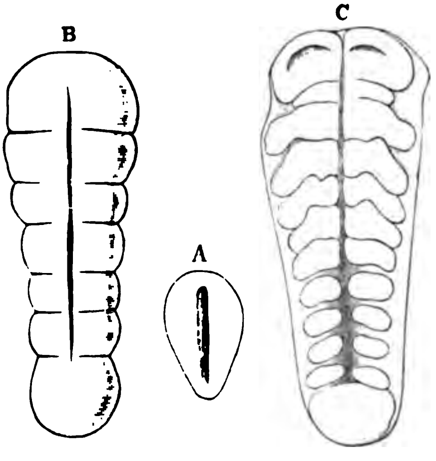

Fig. 4.—*Euscorpius italicus.* *A*-*C*, germ-discs with the median longitudinal furrow (*A*) and germ-bands (*B* and *C*) (after Metschnikoff, from Balfour's *Text-book*). In *B* and *C* the neural groove can be seen, and in *C* the crescent-shaped cephalic pits, and behind them the rudiments of the cephalo-thoracic and abdominal limbs.

Metschnikoff describes a stage in which the embryo seems divided up into three primary regions. The anterior region corresponds to the primary cephalon, and the posterior to the post-abdomen; the middle section is said to give rise to the remainder of the body. This view could not be definitely proved by Metschnikoff, and it is more probable that all the trunk-segments are derived from the posterior region. These early stages of the segmented germ-band show a certain similarity with the ontogenetic stages of the Trilobita, and might thus give rise to a comparison with these forms (Vol. ii., p. 340).

In *Euscorpius*, a stage was observed at which were present the primary cephalic region, a smaller segment following this (that of the

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* [Brauer's App. to Lit. on Scorpiones, No. II.) observations on the origin of the embryonic envelopes in *Euscorpius* are in agreement with those of Laurie. Brauer's account of the whole ontogeny is most complete.—Ed.]

chelicerae), a large segment (that of the pedipalps), another in the act of forming (that of the first pair of limbs), and, finally, a large caudal region. By the separation of other segments from the latter, the number of body-somites is increased. The most anterior of these, with the exception of the primary trunk-segment, seem the most developed. They become less distinct as the caudal region is approached. A furrow appearing in the middle line (neural groove), which is concerned with the formation of the ventral chain of ganglia, and is in no way connected with the median longitudinal furrow already mentioned, divides the germ-disc into two symmetrical halves (Fig. 4 *B*). The similarity between this embryonic rudiment and the germ-band of other Arthropoda and of *Peripatus* is now very pronounced. The germ-band lies upon the yolk, with its ventral surface turned outwards. In the region occupied by the germ-band, which includes the greater part of the germ-disc, the latter appears much thickened (Fig. 3 *B*): the germ-layers spread over the yolk beyond the germ-band, but there appear much less developed. They gradually grow round the whole of the yolk, which thus comes to lie inside the embryo.

The circumcrescence of the yolk by the cell-layers, which have long been differentiated as germ-layers, cannot be regarded as gastrulation, as was thought by BALFOUR. Neither does the blastopore lie on the dorsal surface, but is rather to be sought on the ventral surface, in the middle of the germ-disc (p. 2).

When about ten segments have appeared (METSCHNIKOFF), or perhaps earlier (LAURIE), the limbs become apparent. They arise as outgrowths of the segments on each side of the middle line (Figs. 4 *C* and 6), and are hollow and truncated, the primitive mesoblastic segments which have already attained development lying for the most part within them, a feature which we shall find exactly reproduced, not only in the Araneae, but in *Peripatus* and in the lower Insects. The development of the limbs also takes place from before backward, but the chelicerae are remarkably late in developing (Fig. 4 *C*). When the pedipalps are already large, the chelicerae are no more than small prominences (Fig. 6). This must be explained by their smaller size in the adult. The chelicerae as well as the pedipalps are without doubt post-oral in position, for the mouth first appears quite anteriorly between the cephalic lobes (Fig. 6, *m*). In front of the mouth, an unpaired structure, the upper lip (or rostrum), appears later (Fig. 7 *B*). The rudiments of the four pairs of limbs which follow greatly resemble the chelicerae and pedipalps both in form and in position (Figs. 5 and 8). The series of thoracic limbs is followed by another series of six pairs of abdominal limbs. [In front of these is a small limbless segment (**Brauer**).] The first pair is specially small, and soon degenerates, the slight prominence covering the genital aperture (genital operculum) taking the place of these limbs, while the second pair gives rise to the large combs (Fig. 7 *C*, *pe*). The four posterior pairs also abort, but first become connected with the formation of the lung-sacs, as will be described later (Fig. 8, ap^3–ap^6).

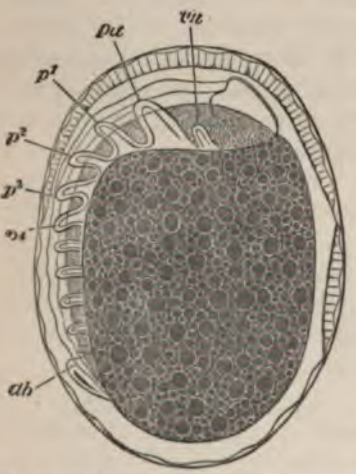

FIG. 5.—Embryo of *Euscorpius italicus* enveloped in its membranes, between which fine filaments stretch (after **Metschnikoff**, from **Balfour's** *Text-book*). The germ-band is seen in profile, lying upon the yolk. *ab*, the post-abdomen bent round anteriorly; *ch*, chelicerae; *pd*, pedipalps; p_1–p_4, the four ambulatory limbs, and, behind them, the abdominal limbs.

While the number of segments and limbs increases in the germ-band, the position of the latter in relation to the yolk changes somewhat. By continuous growth, it finally covers almost half of the oval yolk. As the anterior end grows specially large, the cephalic lobes extend round the yolk, and the germ-band now appears bent round the anterior pole of the egg (Fig. 13 *A* and *B*, p. 22). The posterior end of the germ-band, on the other hand, grows out from the egg and bends downwards and forwards, and the post-abdomen continues to grow with its ventral surface turned to the ventral surface of the germ-band. On its ventral surface a furrow is apparent; this is the continuation of the neural groove (Fig. 7 *B*). Five segments form in it at a later period, the unsegmented telson remaining as the terminal joint (Fig. 7 *C*). In the germ-band proper, the ventral chain of ganglia now appears as a series of distinct segmental thickenings (Fig. 7 *A* and *B*). Long before the germ-band has developed to this extent, the germ-layers outside it have extended further over the yolk; this extension of the blastoderm consists not only of the ectoderm, but also of the entoderm, which is composed of large cells underlying the former, and in this manner the yolk is gradually enclosed.* In the course

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* *Cf.* the detailed account of the formation of the intestinal canal, given below (p. 19).

of development, the yolk becomes absorbed by the entoderm, probably after the yolk-cells scattered throughout the former have brought about its liquefaction. The enteron formed by the circumcrescence of the yolk by the entoderm becomes connected with the stomodaeum, which is formed between the cephalic lobes (Figs. 6 and 13 *B*, *m*). The proctodaeum also arises from a depression of the ectoderm situated on the ventral surface of the telson (according to KOWALEVSKY and SCHULGIN on the penultimate segment). The mesoderm also extends with the growth of blastoderm over the yolk, and, starting from the ventral surface, grows upward between the ectoderm and the entoderm. The development of the embryo thus progresses from the ventral surface, which was formed early, towards the dorsal surface, until at last this also is completely covered.

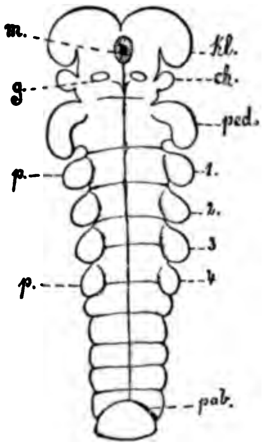

FIG. 6.—Germ-bands of *Euscorpius italicus* (after LAURIE). *ch*, chelicerae; *g*, ganglia of the cheliceral segment; *Kl*, cephalic lobes; *m*, mouth; *p*, ambulatory limbs; *pab*, the post-abdomen bent forward; *ped*, pedipalps; *1*, *2*, *3*, *4*, first four limbs.

It appears as if the extension of the embryonic rudiment over the yolk was accompanied by an outward displacement of the primitive attachment of the embryonic envelopes, so that these finally surround the whole embryo. According to METSCHNIKOFF, they become entirely detached from the embryo, evidently after the enclosing of the yolk, and then form an isolated bilaminar envelope around it. METSCHNIKOFF also confirms GANIN'S view, that between the inner envelope and the embryo another fine cuticular membrane is secreted by the latter, and becomes detached. This would represent a larval integument, such as occurs in the Araneae and Acarina. The embryo is born surrounded by the embryonic envelopes, and escapes from them only after birth (METSCHNIKOFF).

The limbs of the embryo, up to this point, are merely truncated appendages. The pedipalps now become forked, and thus attain their chelate character (Fig. 7 *B*); the chelicerae undergo the same development. Both these pairs of limbs shift towards the mouth and lie at its sides. At the base of each of the pedipalps and of the four pairs of limbs there soon appears an outgrowth, which at first is somewhat large, and is directed towards the middle line; out of this the masticatory blade-like appendage of these limbs is developed. These blades, as we have shown, are of importance in comparing *Scorpio* with *Limulus*. It is a significant fact that the embryo, according to **Laurie**, has these appendages on all the four pairs of limbs, while in the adult they are found only on the first two pairs (in the Pedipalpi on the second pair only (*Phrynus*)).

With the segmentation of the limbs, which takes place somewhat late (in the stage depicted in Fig. 7 *C*), the embryo approaches

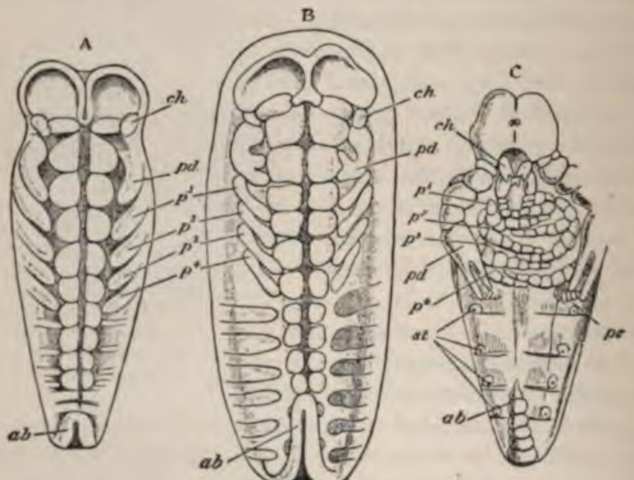

Fig. 7.—Three embryos of *Euscorpius italicus* (after **Metschnikoff**, from **Balfour**'s *Text-book*). *ab*, post-abdomen; *ch*, chelicerae; *pd*, pedipalps; p^1-p^4, the four ambulatory limbs; *pe*, the pectines (combs); *st*, stigmata. In the middle line is the neural groove, and at its side the rudiment of the ventral chain of ganglia. The cephalic pits are visible on the cephalic lobes in *A* and *B*, and the median eye in *C*. The transverse markings on the abdomen are the result of the internal segmentation caused by the primitive mesodermal segments.

the adult form (Figs. 8 and 7 *C*). The limbs lengthen at the same time, and the rest of the body undergoes the modifications described above. The appendages of the first abdominal segment [second according to **Brauer**] degenerate, while those of the second segment [third of **Brauer**] increase in size and develop transverse furrows, which indicate that we have here the rudiments of the pectines (combs). Important modifications occur in the four following pairs of limbs, invaginations, which lead to the development of lungs, forming on their dorsal sides (**Laurie**). As these invaginations form, the abdominal limbs themselves gradually degenerate. In the embryo depicted in Fig. 8, the abdominal limbs can still be recognised, while, in Fig. 7 *C*, the four pairs of stigmata are already visible.

The origin of the lungs as invaginations on the dorsal side of the abdominal limbs is a point of importance in comparing the Scorpiones with *Limulus*, since this ontogenetic feature is referable to the drawing of the branchial lamellae into the body. Although we feel inclined to adopt this point of view, it appears to us that the proofs brought forward by LAURIE in support of this important point are not sufficient, and that the whole subject requires more careful and thorough investigation than it has received in his treatise. It cannot be denied that the relation of the lung-invaginations to the abdominal limbs is very striking. This is evident from Fig. 8, after METSCHNIKOFF, although this author remarks that the lung-invaginations are not derived from the limbs, but arise at the points where the abdominal limbs have disappeared.

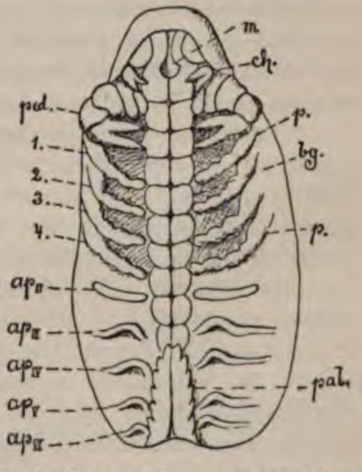

FIG. 8.—Embryo of *Euscorpius italicus* (after METSCHNIKOFF). *1-4* (*p*), the four pairs of limbs; ap_{II}–ap_{VI}, abdominal limbs [*III–VII*, BRAUER]; *bg*, ventral chain of ganglia; *ch*, chelicerae; *m*, mouth; *pab*, post-abdomen; *ped*, pedipalps.

Behind the last stigmata-bearing segment another pre-abdominal segment develops, this being followed by the post-abdomen of five true segments and the telson. The post-abdomen is still bent round ventrally (Fig. 7 *C*). The telson has developed at its end, and two ectodermal invaginations give rise at its point to the paired poison glands, which in the adult still open through two apertures at the tip of the telson. The anus appears as an ectodermal invagination at the end of the last true segment of the post-abdomen.

By means of the modifications just described, the embryo attains the general form of the adult, these external changes having been accompanied by development in the internal organs, which will be described later, and in the covering of the body, chief among these being the secretion of the chitinous cuticle. At the time of hatching, the young Scorpion raises its post-abdomen (tail) over its back, thus completing its resemblance to the adult.

3. The Formation of the Organs.

A. The Nervous System and the Eyes.

The ventral longitudinal commissures arise early in the form of two thickened bands situated at the sides of the median groove, and extending the whole length of the body (Fig. 7, *A* and *B*). A segmentation into the ganglia is soon apparent. The increase in size of these ganglia (according to KOWALEVSKY and SCHULGIN) is due to the development of ten to twelve pit-like depressions on each segment, these representing points of specially active cell-growth. Fifteen to twenty such depressions are also found on the cephalic segment. They suggest the vestiges of sensory organs, which finally disappear when the chain of ganglia becomes detached from the ectoderm. The invaginated median strand (the neural groove) also seems to participate in the formation of the ventral chain of ganglia (PATTEN, LAURIE), but this point is not yet established. We are unable to determine from the statements of the above authors whether the chain of ganglia and the supra-oesophageal ganglion form one continuous rudiment, or whether these two parts of the system arise separately.

The **supra-oesophageal ganglion** seems to arise in close relation to the invaginations which were evident in earlier stages, first as rounded, and then as semi-circular depressions on the cephalic lobes (Fig. 4, *C*, and 7, *A* and *B*). While these cephalic pits are still shallow, a distinct thickening of the ectoderm takes place between them (Fig. 12, *A*). This forms the median wall of the two pits. We may assume that this thickening is chiefly concerned in the formation of the brain. Later, the pits become deeper, their apertures become narrower, and shift backwards, as will be further described in connection with the formation of the eyes. It appears that the rudiment of the brain at the same time becomes gradually detached from the pits, and takes up a more lateral position. This accounts for the fact that, at a later stage, the rudiment of the brain lies laterally to the pits. The cephalic pits furnish the rudiments of the median eyes.

The above description does not altogether agree with statements made by LAURIE, KOWALEVSKY, and SCHULGIN, who regard the brain as more closely connected with the depressions, indeed, as directly derived from them. We are not able, however, to interpret the figures given by LAURIE and PATTEN in any other sense. There would still be a connection between the formation of the brain and that of the median eyes, but it would not be so close as the authors above-named imply.

In the rudiment of the brain, and especially in those parts of the cephalic pits which take part in its formation, there occur the same small depressions which were mentioned above in connection with the formation of the chain of ganglia, and were regarded as the formative area for ganglionic cells (Kowalevsky and Schulgin, Laurie). When the brain separates from the cephalic pits, it seems at the same time to lose its connection with the ectoderm.

With the brain are united the ganglia of the cheliceral segment (Kowalevsky and Schulgin), a corresponding connection being found in the adult. The two pairs of cheliceral nerves thus have their origin in the brain, which is divided into an anterior portion, giving origin to the optic nerves, a small middle unpaired portion giving origin to the nerves of the rostrum, and a posterior paired portion giving origin to the cheliceral and sympathetic nerves. The thoracic ganglia and those of the first two [? three] abdominal segments unite to form the large sub-oesophageal ganglionic mass in the thorax which approximates to the brain. The number of abdominal ganglia becomes reduced, by this fusion of some of the anterior pairs, to seven (four probably belonging to the pre-abdomen, and three to the post-abdomen). Some of the above facts were made known through the researches of H. Rathke (No. 28) as early as 1837.

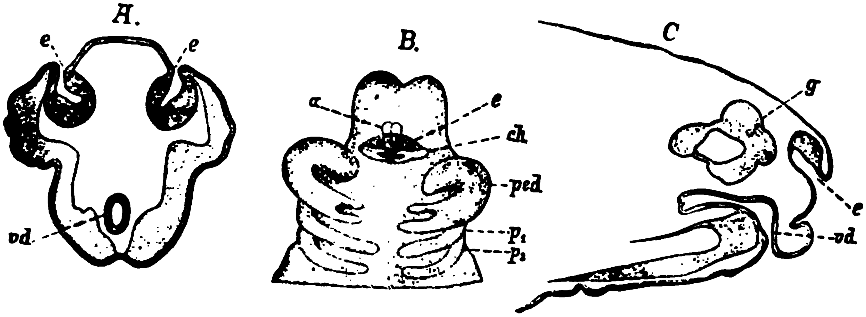

Fig. 9.—*Euscorpius italicus* (after Laurie). *A*, transverse section through the anterior part of the embryo; *B*, anterior part of an embryo spread out flat, and seen from the ventral side; *C*, sagittal section through the head. *a*, rudiment of the median eyes (lenses); *ch*, chelicerae; *e*, cephalic pits; *g*, brain; p_1, p_2, first and second ambulatory limbs; *ped*, pedipalps; *vd*, stomodaeum.

The **formation of the median eyes** is connected with that of the supra-oesophageal ganglion, inasmuch as both can be traced back, in part at least, to the cephalic pits. It has already been stated that these pits are said to take part in the formation of the brain. It is probable that, before the complete separation of the brain from the cephalic pits, the apertures of the two invaginations (Fig. 9, *A*, *e*) shift backward and towards the middle line, so as to fuse later to form a common depression. This change is evidently due to a process of growth, by which that portion of the body lying between the pits is gradually drawn into them. If we rightly understand Laurie's description, the common pit seems to be of large extent, but rather shallow (Fig. 9, *B*, *e*). It lies immediately in front of the chelicerae which have already developed as pincers.

The position of the chelicerae in relation to the cephalic pit is somewhat difficult to determine from the illustrations available. In Fig. 12, the pits at several stages are indicated in outline; but unfortunately Patten's description does not enable us fully to understand his figure.

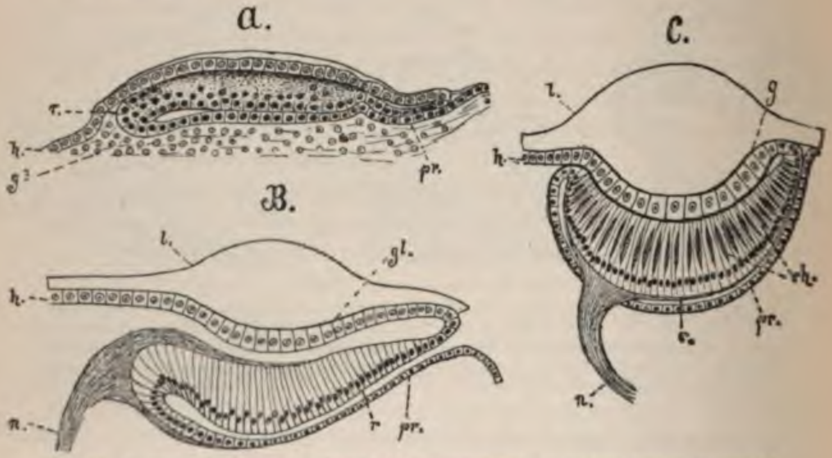

Fig. 10.—Sections through three stages of development of the median eyes in *Scorpio* (*A*, after Parker, *B* and *C*, diagrammatic). *g*, brain (?); *gl*, vitreous body; *h*, hypodermis; *l*, lens; *n*, optic nerve; *pr*, post-retinal layer; *r*, retina; *rh*, rhabdom.

The outer edge of the pit grows towards the middle line, thus roofing it in and causing an approximation and ultimate fusion of the two apertures, and the formation of a single bilobed pit in place of the two originally distinct ones (Figs. 9, *C*, and 12, *F*). The outer wall of the pit lying under the ectoderm or hypodermis thickens (Fig. 9, *C*), while the inner wall remains thin and unilaminar. The whole depression, which is somewhat closely apposed to the hypodermis, becomes flattened dorso-ventrally, so as to appear like a flat pouch (Fig. 10, *A*). A right and a left portion can, however, be recognised, and each of these portions corresponds to the rudiment of one of the eyes.

The dorso-ventral flattening undergone by the common optic pit considerably diminishes the size of its cavity, of which, finally, only traces can be found (Fig. 10, *A*). The external aperture also closes completely. The thickened upper wall of the optic pit is now in close contact with the hypodermis (Fig. 10, *A*, *r*), and pigment has already appeared in it. It represents the retina of the eye, and, later, by gradual differentiation, yields the groups of retinulae, as well as the pigment-cells between them. The hypodermal layer (*h*) which lies over the retina becomes the vitreous body, and secretes the lens externally; it has therefore recently been designated as the lentigen layer (MARK). The cell-layer lying behind the retina, *i.e.* the lower wall of the optic pit (Fig. 10, *pr*), is the post-retinal layer of ectoderm-cells found in the adult. This layer secretes posteriorly the cuticle which surrounds the optic cup (Fig. 10, *C*). The post-retinal layer itself comes into close contact with the retina at a later stage. A cuticle resembling the basal membrane of the post-retinal layer also appears between the cells of the vitreous body and the retina (PARKER). It represents the fused cuticular borders of these two cell-layers and separates them from one another (Fig. 10, *C*).

The innervation of the developing eye is of special interest. It has already been shown that part of each cephalic pit enters into the formation of the brain, and the optic ganglia must, indeed, arise chiefly in this way. In Fig. 12, *B* and *C*, these ganglia are seen connected with the optic pit. Later, they become almost entirely separated from it, retaining only a narrow and drawn-out connection representing the optic nerve (Fig. 12, *C* and *D*). On the inner side the optic ganglia are connected from an earlier stage with the brain (Fig. 12, *A* and *D*).

In the earlier stages in the development of the eye, the optic nerve is at first connected with the convex surface of the optic invagination (PARKER), and the nerve fibres seem chiefly to unite with the surface which is turned towards the hypodermis (Fig. 10, *B*). This surface, however, corresponds to the side of the retina which, in the adult eye, is directed towards the exterior, *i.e.* the nerve-fibres at this stage unite with those ends of the retina-cells which, in the adult eye, are the free ends, and are directed outward. Directly opposite conditions are thus found in the embryo and in the adult, and it must be assumed that the nerve-endings shift, during the course of development, from the outer to the inner ends of the retinal cells (**Mark**, **Parker**). If the above is really the case, these processes are of great histological interest, but these changes need further investigation before they can be regarded as fully established. From a theoretical standpoint, the account just given of the optic nerves is highly suggestive. The rudiment of the eye appears as an invagination, and we should expect that, by the closing of this invagination, the lens and the vitreous body would develop from the outer, and the retina from the inner, wall of the optic pit. The nerve would then join the posterior wall of the eye. This latter is actually the case, but the lens and the vitreous body are formed from a part of the hypodermis lying outside the invaginated area (Fig. 10, *A–C*). A striking modification in the formation of the eye has thus come about, the cause of which is as yet unknown. The result of this modification is that the surface of the retina which, at an early stage, was directed inwards, is now approximated to the lentigen hypodermis (Fig. 10, *B*). With this portion of the optic pit the nerve retains its primary connection. In order that the eye may form according to this new method, however, the nerve must shift from the original convex, lower surface to the primary concave surface of the invagination (Fig. 10, *B* and *C*). A portion of the wall of the pit becomes, during this process, the post-retinal layer, losing its sensory character. This layer must necessarily be traversed by the nerve, as is actually the case in the adult animal (**Ray Lankester** and **Bourne**, No. 20).

The lateral eyes arise much more simply than the median eyes. At the time when these latter arise, two long pigmented areas of the integument appear laterally and somewhat posteriorly to them; these are the rudiments of the lateral eyes. The hypodermis is much thickened at these parts, and a number of depressions appear; there may be as many as five, but the number varies in the different species of *Scorpio* (Fig. 11 *A*, *II–V*). Each of these pits gives rise to an eye, which develops very simply in keeping with the simple structure of the adult lateral eye (**Parker**). The greater part of the invagination becomes the retina. When the lens is formed, the more peripheral cells grow inward over the central portion (retina) and secrete the lens, which now lies over the slightly depressed central part (Fig. 11 *B*). In this latter, we now find differentiated retinal cells and the intercalated pigment cells, while, laterally, this single layer of cells passes gradually into the peripheral (lentigen) cells, which, in their turn, are continued direct into the hypodermis (Fig. 11 *B*). This continuous cell-layer secretes posteriorly a cuticular basal membrane, which separates the eye from the surrounding tissues. The nerve becomes connected with this posterior side of the eye.

While the median eyes of *Scorpio* thus originate as complicated processes of infolding, the lateral eyes arise very simply as mere depressions of the hypodermis. The simpler structure of the lateral eyes is not sufficient to explain this, so that there must be other factors which are not yet rightly understood. In relation to this, the transformation of the cephalic pits into the rudiments of the median eyes is remarkable.

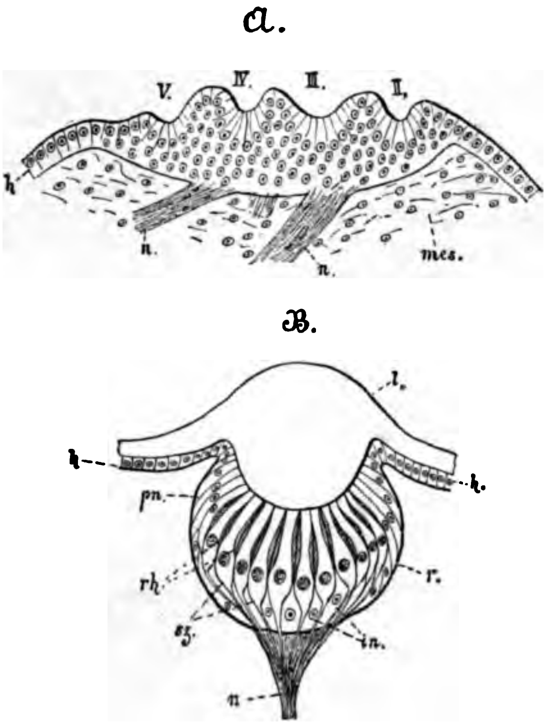

FIG. 11.—Sections through two ontogenetic stages of the lateral eyes of *Scorpio*. *A*, earlier, *B*, later stage; somewhat diagrammatic (after PARKER and LAURIE). *II–V*, the optic invaginations; *h*, hypodermis; *in*, interneural cells; *l*, lens; *mes*, mesodermal tissue; *n*, optic nerve; *pn*, perineural cells; *r*, retina; *rh*, rhabdom; *sz*, retinal cells (terminal cells of the nerve).

We have founded our account of the origin of the brain and the eyes on the descriptions of authors who have investigated this subject, but these are for the most part very incomplete, especially as regards the formation of the brain and the first rudiments of the median eyes. These observers sometimes directly contradict themselves, or else their accounts are rendered quite incomprehensible by paucity of description or of figures. [See **Brauer**'s recent work.]

We must, before leaving this subject, give a brief account of **Patten**'s description of the origin of the brain and eyes, which differs essentially from that given by other authors. **Patten** assumes that the cephalic lobes in *Scorpio* consist of three segments (*cf.* the structure of the brain in the Insecta). Each of these three segments bears two pairs of eyes, a pair of optic ganglia, and a segment of the brain (Fig. 12 *E* and *F*). In each segment two regions can be distinguished, a central, cerebral portion and an external optic region, this again being divisible into an inner portion yielding the optic ganglia, and an external region which yields the eyes ("optic plates"). These regions are thrice repeated from before backward (Fig. 12 *E*). Whereas other authors observed only the two semicircular depressions of the cephalic lobes, **Patten**

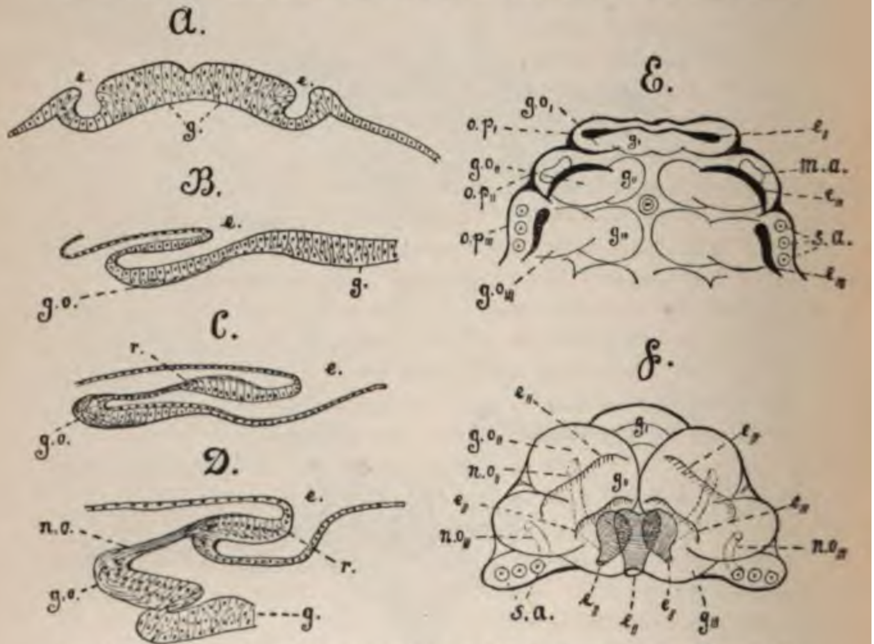

FIG. 12.—*A*, transverse section through the cephalic lobes of *Euscorpius italicus*, showing the two cephalic pits (*e*), somewhat diagrammatic. *B–D*, sagittal sections through the cephalic lobes of *Buthus carolinianus*, showing the formation of the brain and the median eyes. *E* and *F*, plans of the cephalic lobes of the same Scorpion at different stages (*A*, after **Laurie**, *B–F*, after **Patten**). *e*, cephalic pit; $e_{,}$–$e_{,,,}$, the same in the three segments of the cephalic lobes; *g*, rudiment of the brain; $g_{,}$–$g_{,,,}$, the same in the three segments; *g.o*, optic ganglion ($g.o_{,}$–$g.o_{,,,}$ in the three segments); *m.a*, median eyes; *n.o*, optic nerve ($n.o_{,,}$ and $n.o_{,,,}$ in the second and third segments); $o.p_{,}$–$o.p_{,,,}$, "optic plate" of the three segments; *r*, retina; *s.a*, lateral eyes.

describes three pairs of depressions, one in each segment; the one in the middle must be identical with the cephalic pits of other authors, its transformation has already been described (pp. 12–15). *These middle pits give rise simultaneously to the median eyes and the optic ganglia, the latter sinking in with them* (Fig. 12 *E*). *The formation of the optic nerve is thus easy to explain* (Fig. 12 *C* and *D*). The optic ganglia are connected with the cranial part, which has meanwhile also shifted inwards.

The first segment has no eyes, but the third carries the lateral eyes; these, however, are not invaginated. We cannot here follow PATTEN's account further, as his conclusions do not seem sufficiently supported, and his statements are too fragmentary. It is also impossible to decide as to the value of PATTEN's statements, which, as the title of his treatise (No. 27) shows, were made with another object; indeed, his method of description often makes it impossible for us to obtain even a slight idea of the formative processes observed by him.

B. The Lung-sacs.

The lung-sacs arise, as has already been mentioned (p. 11), as depressions on the posterior sides of the last four abdominal limbs (METSCHNIKOFF, LAURIE, Fig. 8, p. 11). These depressions are at first shallow, but then grow deeper and spread forwards, extending in front of their narrow apertures, which correspond to the future stigmata (Fig. 9 *C*, *st*). The sacs project into a vascular mesodermal cavity (KOWALEVSKY and SCHULGIN, LAURIE).

The assumption of the adult form by the lung-sacs takes place in the latest embryonic stages; it commences by the occurrence of depressions in their inner walls. These lead to the formation of folds which grow out further and further into the cavity of the sac (*i.e.* posteriorly). Other folds form, and the lamellate structure of the sacs thus gradually arises (LAURIE). The wall of the embryonic lung-sac consists of a cylindrical epithelium (hypodermis), which secretes a fine cuticle on the surface turned towards the cavity of the sac (METSCHNIKOFF).*

We shall deal further with the development of the lung-sacs and their morphological relations when we come to treat of the respiratory organs of the Araneae (p. 76).

C. The Intestinal Canal.

The enteron develops somewhat differently in the different regions of the body. While the entoderm is represented by a single layer of cells wherever it surrounds the yolk, in the post-abdomen it first appears as a solid cell-mass (Fig. 13). In the post-abdomen, the

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* [LAURIE (App. to Lit. on Scorpiones, No. IV.) states that the lamellae of the lung-book in the embryo lie horizontally and parallel to the ventral surface, while in the adult the lamellae are arranged parallel with the axis of the body and perpendicular to the ventral surface. He supports MACLEOD's rather than LANKESTER's view concerning their origin.—ED.]

enteron first develops fully, arising from this cell-mass in the form of a tube which, like this body-region itself, is at present neither thick nor long. The gut continues to develop from this region, the epithelium differentiating first on the ventral surface, and gradually extending dorsally. The whole of the yolk was surrounded by entoderm at an earlier stage, but it appears that the cells of the entoderm resemble those we have already met with in the Crustacea (Vol. ii., p. 129). They are greatly swollen and are of a cylindrical shape, so that they do not yet resemble the future intestinal epithelium; they are chiefly occupied in the assimilation of the yolk. This provisional epithelium gradually changes into the definite intestinal epithelium from behind forward, first developing ventrally, and then extending towards the dorsal side. The hepatic caeca, which at first contain abundant masses of food-yolk, form as outgrowths of the provisional epithelium, perhaps also caused by the inward pressure of the folds of the splanchnic layer of the mesoderm, as in the Araneae (p. 82). It appears as if the hepatic tubes were segmentally arranged. By further extension and ramification, the liver attains its definite form.

It seems probable that the above description of the development of the enteron is correct, since **Laurie**, as well as **Kowalevsky** and **Schulgin**, speak of a somewhat early and complete circumcrescence of the yolk by the entoderm. We have not, however, succeeded in obtaining a perfectly clear idea of these processes from the works of these observers. They might be understood to imply that the circumcrescence just mentioned is only complete at some parts, *e.g.* anteriorly, where the germ-band grows round the pole of the egg, and especially posteriorly, and that the circumcrescence of the yolk by the entoderm only takes place from behind (progressing ventro-dorsally), the entoderm soon developing into the definitive intestinal epithelium. This method of origin of the intestine would somewhat resemble that in the Araneae, where the epithelium of the enteron grows round the yolk-mass, which is directly bounded by mesoderm (p. 82). We are not, however, able to obtain this idea from the treatises under review, and there would even then be considerable difference between this process and that in the Araneae, since, in the latter, the first rudiment of the enteron is said to form from an accumulation of yolk-cells.

The two long, tubular intestinal appendages which until now have been called *Malpighian vessels*, and thus regarded as homologous with the synonymous organs of the Insects and Myriopoda, arise in the last segment of the pre-abdomen as outgrowths of the enteron (**Laurie**). The two outgrowths form comparatively far forward on the enteron at a time when the proctodaeal invagination has not yet appeared. When this arises, the Malpighian vessels are seen opening into the intestine in the pre-abdomen; their point of origin is thus far removed from the proctodaeum. This is not the case in the Araneae, in which the so-called Malpighian vessels arise close to the point where the enteron and the proctodaeum unite. In the Scorpiones also the large section of the intestine lying behind the point where the Malpighian tubes enter it has been regarded as the proctodaeum, *i.e.*, looked upon as of ectodermal origin. If LAURIE's observations should prove correct, this section, or at any rate the greater part of it, must be considered as entodermal, and the proctodaeum proper would then also be very short in the adult; a decided shifting of the Malpighian vessels must then have taken place.

Although KOWALEVSKY and SCHULGIN do not mention the origin of the Malpighian tubes, their statements as to the origin of the enteron and the proctodaeum agree with LAURIE's view. According to them, the tubular posterior part of the enteron grows through the whole of the post-abdomen to the penultimate segment, where it joins a short proctodaeum. But for this statement, we might be inclined to suppose that the portion of the intestine lying in the post-abdomen was of ectodermal origin, and to assume that the proctodaeum ran very far forward, especially as the proctodaeum in the Araneae is very long. Such an assumption, however, is incompatible with the descriptions of LAURIE and of KOWALEVSKY and SCHULGIN. We must therefore regard the so-called Malpighian tubes of the Scorpiones as entodermal, although we must point out the desirability of further research in connection with this important point. The Malpighian vessels of the Myriopoda and the Insects arise undoubtedly from the ectoderm, *i.e.*, they are appendages of the proctodaeum. In a few Crustacea, on the other hand (*e.g.*, the Amphipoda), tubular appendages are found at the posterior part of the enteron, which are probably excretory, and resemble the Malpighian vessels in structure.

The stomodaeum arises as an invagination between the cephalic lobes (Figs. 6 and 13 *B*). The proctodaeal invagination which, according to LAURIE, appears at a very late stage, seems to be shifted towards the penultimate segment; this corresponds to the position of the anus in the adult. The two ectodermal organs, the stomodaeum and the proctodaeum, only unite with the enteron at a later period. Indeed, the intestine develops so late that, when the embryo is ready for birth, its cells have not yet attained the regular epithelial arrangement of the anterior part of the enteron, but some of them still extend in between the masses of yolk. The cells are not distinctly marked off internally, and the lumen is not yet formed. This incomplete development of the intestine, and the presence of a quantity of yolk within it, render it highly probable that the young Scorpion does not begin to feed for some time after birth. The mother is known to take care of the brood also after birth, carrying the young about on her back for some time.

D. The Mesodermal Derivatives.

Our information as to the origin of the mesodermal structures is very slight; but from what is known of the differentiation of the mesoderm-bands, it appears to be very primitive. The two mesoderm-bands break up into a number of somites, corresponding to the segmentation of the body, these somites developing from before backward (Fig. 13, *h* and *mes*), those of the post-abdomen being the last to form. A well-developed pair of these primitive mesodermal segments occurs in the (primary) cephalic region (Fig. 13 *A*). At first the primitive segments lie at a little distance from the ventral middle line (Fig. 3 *B*), but they grow in towards it later.

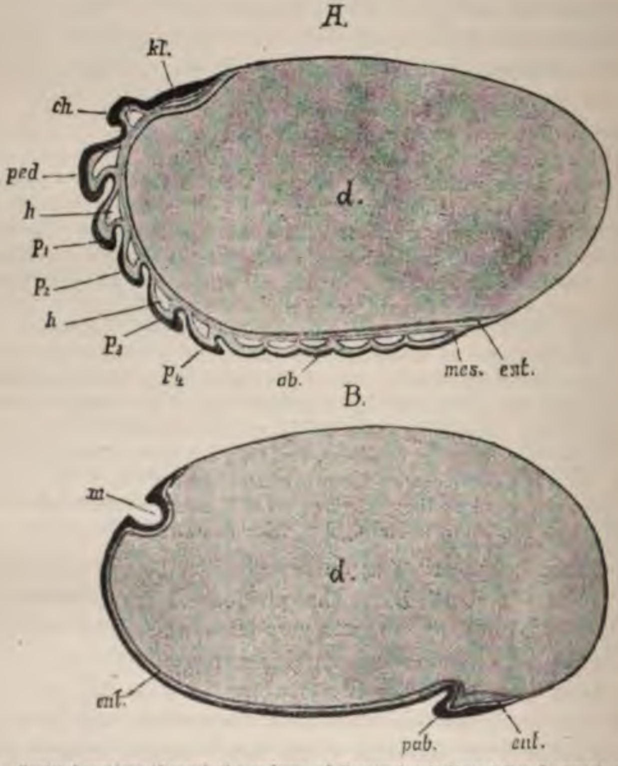

FIG. 13.—Sagittal sections through the embryo of *Euscorpius italicus* (after LAURIE), to show the dorsal curvature of the germ-band. *A*, near the middle line; *B*, median section. *ab*, abdomen; *ch*, chelicera; *d*, yolk; *ent*, entoderm; *h*, cavity of the primitive segments; *kl*, cephalic lobe; *m*, mouth (stomodaeum); *mes*, mesoderm; p_1-p_4, first four limbs; *pab*, post-abdomen; *ped*, pedipalp.

Their extension towards the dorsal surface is, however, specially noticeable. While this dorsal extension is less marked in the anterior segments, it is very striking in the abdomen, where the primitive segments soon grow beyond the area of the germ-band towards the dorsal side. This is well marked in the posterior region in Fig. 7 *B*, though these segments are shown somewhat too distinct. As the anterior segments undergo the same process, the whole of the mesoderm, pressing forward between the ectoderm and the entoderm, extends dorsally. The outer wall of the primitive segments (the somatic layer), is now thicker, being composed of several layers of cells, while the inner wall (the splanchnic layer) consists of a single layer of cells. The pair of primitive segments in the cephalic region has specially thin walls, the lumen also being comparatively small (LAURIE).

The extension of the mesoderm dorsally is not caused by the mere enlargement of the primitive segments with their cavities, but this extension progresses in such a way that, dorsally, where the somatic and splanchnic layers unite, the common rudiment continues to grow upwards as a single layer of cells (KOWALEVSKY and SCHULGIN). This more dorsal portion of the mesoderm does not split up until later, when there is formed in each segment another pair of segmental cavities, the walls of which now meet in the dorsal middle line (LAURIE). We thus find that the differentiation of the mesoderm in the Scorpiones is very primitive, and strongly recalls the similar process in the Annelida. A similar condition is also found in the Araneae. Before the development of the primitive segments has advanced thus far, the rudiment of the heart is said to appear.

E. Blood-vascular System and Coelom.

The **heart**, according to KOWALEVSKY and SCHULGIN, develops from the paired layer mentioned above as proceeding from the dorsal union of the somatic and splanchnic mesoderm. These grow on either side towards the dorsal middle line, where they unite. At the same time they seem to bend upwards, each forming half of a tube open towards the entoderm, which extends from the head to the tail of the embryo. When this half tube closes on its lower side, the formation of the dorsal vessel is practically completed. The anterior part of it, which lies in the cephalo-thorax, and the most posterior part no doubt yield the anterior and posterior aortae.

In the cavity of the heart there are many isolated cells which became detached from the primitive segments before they extended dorsally. These cells yield the blood-corpuscles. A similar process has been observed in the formation of the heart of the Araneae (see Figs. 45–47, pp. 86–89).

The description of the origin of the heart given by **Kowalevsky** and **Schulgin** is not altogether easy to reconcile with that given by **Laurie**. The statements of the former seemed so definite that we felt obliged to follow them; but, on the other hand, the observations of **Laurie** agree better with the processes which take place in the Araneae. It is, in fact, impossible to obtain a clear idea of the whole process from the works under consideration. According to **Laurie**, it appears as if the dorsal part of the mesoderm had already split when the formation of the heart begins, in which case this organ would develop as in the Araneae. We are, moreover, disposed to regard the process as resembling that in the Annelida, and to imagine a delamination of the mesoderm to form the heart; this organ, however, is thought to arise somewhat differently in the Araneae (p. 88).

Kowalevsky and **Schulgin** distinguish an endothelium and a muscle-layer in the heart, both arising from the mesoderm. During the differentiation of these layers, the ostia appear in the wall of the heart. The alary muscles form from the mesoderm, and a layer of mesoderm-cells appears around but at a little distance from the heart, forming a continuous envelope to it; this is the pericardium.

The **coelom** of the Scorpiones, up to the time when the heart forms, closely resembles that of the Annelida. It consists at first of separate divisions formed in the primitive segments. The anterior and posterior walls (dissepiments) of the latter are broken through, but the cavities themselves are retained for a time, and are lined by the coelomic epithelium; they thus represent a true coelom. At the time when outgrowths of the splanchnic layer extend in between the lobes of the liver, this is, according to **Laurie**, still the case. These cavities then become filled with cells, which doubtless arise during the disintegration of the wall of the primitive segments. The somatic layer undergoes further differentiation, the body-musculature forming out of it. The coelom will be further described in connection with the development of the Araneae, in which it is better known than in other Arachnids.

F. The Coxal Glands.

A complicated coiled gland is found on each side of the cephalothorax in the Scorpiones, opening, in the young, on the base of the third ambulatory limb (Fig. 14, *A*). At its earliest stage, this gland is described by **Laurie** as a simple, straight tube, which runs forward from its aperture at the base of the third ambulatory limb in the somatic layer of the mesoderm, and communicates with the coelom *through a funnel-shaped aperture.* The tube becomes closely coiled later, finally forming the glandular mass which is found in the adult. The external aperture was still evident in the young when ready for birth. This latter point was confirmed by Kowalevsky and Schulgin, who observed the gland both in its earlier slightly coiled stage and in its later more compact condition. [See Brauer, No. II.]

The structure and position of the coxal glands in the youngest known stage render it highly probable that they are formed from the somatic mesoderm. They are assumed to be nephridia, a view which seems very probable. Considering the primitive character of the coelom in the Scorpiones, we should expect the nephridia to open into the body-cavity through funnels, and this is actually the case for a time. The further development of the inner terminations of the gland must depend essentially on the modifications undergone by the body-cavity, but this point is somewhat obscure. More thorough ontogenetic researches are required before it can be stated with certainty whether, as in *Peripatus* and the Crustacea, a part of the body-cavity forms a capsule for the formation of the terminal sac of the gland, or whether the mouth of the funnel is retained for a considerable time in a wide secondary body-cavity. The most recent writer on this subject, Sturany (No. 14) was not able to prove that the coxal glands in the Arachnida opened into the body-cavity, and he inclines to believe in the presence of a closed terminal sac, such as is found in the Crustacea, but here also we must demand actual proofs.

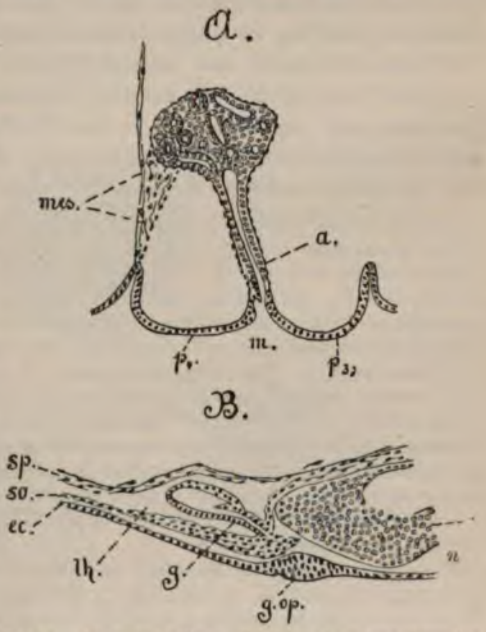

Fig. 14.—*Euscorpius italicus.* Portions of sections through a newly-hatched Scorpion (*A*) and an advanced embryo (*B*) to show the coxal gland and the formation of the genital organs (after Laurie). *a*, efferent duct of the coxal gland; *ec*, ectoderm; *g*, efferent duct of the genital organ; *g.op*, genital operculum; *lh*, body-cavity; *m*, external opening of the coxal gland; *mes*, mesoderm; *n*, ventral nerve-cord; p_3, p_4, bases of the third and fourth limbs; *so*, somatic, *sp*, splanchnic layer of the mesoderm.

G. The Genital Organs.

The ontogeny of the genital organs has as yet been little investigated. They were first observed by Laurie at a late stage of development shortly before birth, in the first abdominal segment [second, Brauer], as tubular structures at first unconnected with the exterior (Fig. 14 *B*). Kowalevsky and Schulgin, who also noticed them, referred them, though with some hesitation, to the splanchnic layer of the mesoderm. Laurie's account would rather tend to show that they arise from the somatic layer, as do the coxal glands of the Scorpiones and the nephridia of the Annelida (Vol. i., Fig. 137, p. 297). The nephridial character of the efferent genital ducts seems to be confirmed by the fact that they open into the body-cavity in the form of a wide funnel (Kowalevsky and Schulgin [Brauer]). Laurie also believes that at least in part they are nephridial in origin. The ends of the canals which are directed outwards long remain closed, a fact which we do not regard as disproving the nephridial character of the efferent ducts, since even the Annelidan nephridia develop in a similar way.

From Laurie's description we might imagine that the mesodermal efferent ducts become directly connected with the ectoderm at the points where the remains of the first pair of abdominal limbs lie in the form of ectodermal thickenings (Fig. 14 *B*, *g.op*), as is the case, according to Bergh, with the nephridia of the Annelida. Kowalevsky and Schulgin, however, speak of an ectodermal invagination, towards which the mesodermal efferent duct grows, so as to unite with it. This invagination, as far as can be made out from their short account, is small, and it appears very possible that such an ectodermal invagination might arise at the thickening which indicates the position of the abdominal limbs. An ectodermal termination has also repeatedly been assumed for the nephridia and the genital efferent ducts of the Annelida. It is, however, highly probable that the short unpaired portion is derived from a depression of the ectoderm. In the Pedipalpi this unpaired segment is much larger, and becomes a large cavity (No. 31).

The genital glands arise, according to Kowalevsky and Schulgin, as cell-thickenings "apposed to the inner tube." This can only be understood to mean that a part of the peritoneum (*i.e.*, of the secondary body-cavity) is concerned in the formation of the genital organs; on this point, however, as well as on the differentiation of the mesodermal structures, we await further particulars.*

II. Pedipalpi.†

According to Bruce, who has made a few statements as to the ontogeny of *Phrynus*, the embryo here, as in the Scorpiones, has an embryonic envelope. We may indeed make the general assumption that the course of development in the Pedipalpi resembles that in the Scorpiones. Bruce points out as specially remarkable the existence of a sensory organ at the base of the second ambulatory limb, consisting of columnar cells prolonged externally into filaments.

The Pedipalpi are very closely related to the Scorpiones, and, like the latter, show in their organisation many points of agreement with

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* [See footnote, p. 3.—Ed.]

† [The Pedipalpi are oviparous; the eggs are carried in a gelatinous sac attached to the ventral surface of the mother. For chief ontogenetic features see App. Lit. Pedipalpi, Nos. I.–III., noting presence of *reversion* of germ-bands and unanimous conclusion that Pedipalpi are more nearly related to the Araneae than to the Scorpiones.—Ed.]

Limulus (Ray-Lankester, Bruce). Our knowledge of the ontogeny of the Pedipalpi is unfortunately very incomplete, and this may also be said of *Koenenia mirabilis*, a form discovered by Grassi (under stones in the plains of Catania), which shows great resemblance to the Pedipalpi, but has been placed by him in a separate order, the Microtelyphonidae, the Palpigradi of Thorell.* This form is said to have no special respiratory organs, and Grassi therefore sees in it a transitionary form between the Gigantostraca and the Arachnida, which has "already lost the gills, but has not yet developed respiratory organs suited to a terrestial existence"! We can hardly imagine such a transition, and would rather regard the absence of respiratory organs, if it actually occurs, as a degeneration, such as is met with in other air-inhabiting Arthropoda in cases where the body is distinguished from related forms by its specially small size (*e.g.*, in a few Mites, among the Arachnida, and in *Pauropus* among the Myriopoda).

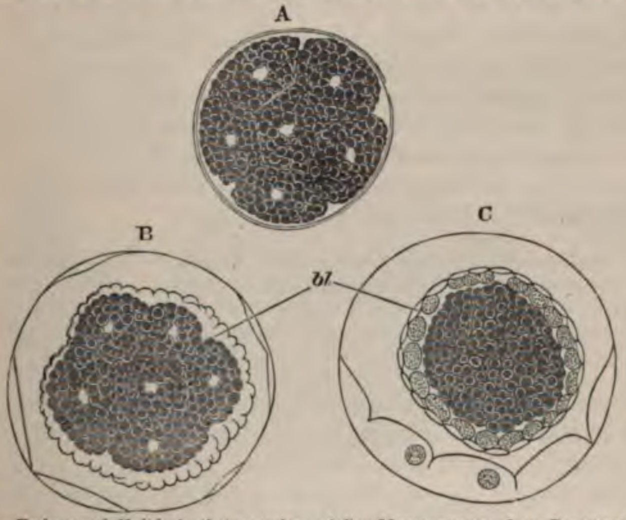

Fig. 15.—Embryos of *Chelifer* in their envelopes (after Metschnikoff, from Balfour's *Text-book*). *A*, early cleavage stage. *B*, stage in which the blastoderm (*bl*) has separated from the yolk-masses within. *C*, splitting of the blastoderm into two layers. The yolk-masses are seen within the egg. A cell-like albuminous tissue appears between the blastoderm and the egg-integument.

III. Pseudoscorpiones.

The little that is as yet known of the ontogeny of the Pseudoscorpiones does not seem sufficiently well established to enable us to form a decisive judgment with regard to the extraordinary development of these forms. Metschnikoff's

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* [Hansen and Sörensen (App. Lit. on Palpigradi, No. I.) give a very careful account of *Koenenia*, and correct many errors in Grassi's description.—Ed.]

statements as to the development of *Chelifer* up to the time of the formation of the blastoderm are, indeed, confirmed by STECKER with regard to *Chthonius*, but the description of the latter author is not calculated to inspire confidence. A more recent treatise by J. BARROIS * on the ontogeny of *Chelifer* is too short to supply many further details.

The eggs of *Chelifer* and of *Chthonius* are spherical and crowded with yolk-spherules. Each is surrounded by a vitelline membrane, and again by a second envelope probably secreted by the oviduct. These eggs are carried by the mother on the ventral surface of the abdomen, where they pass through their development. The cleavage is at first complete, the egg dividing up into two, four, and eight equal blastomeres (Fig. 15 *A*). In the latter stage, *i.e.*, when the egg is divided up into eight spheres, clear protoplasmic segments are said to appear on the surface of the yolk-laden spheres. The number of these clear cells soon greatly increases, until they form a layer surrounding a central mass of yolk (Fig. 15 *B*); this layer may be regarded as the blastoderm. The large yolk-segments with their nuclei can still be clearly seen within the egg.†

The whole process must, no doubt, be thus explained: The few nuclei which enabled the yolk to break up into segments, by division, send off nuclei to the periphery, the nuclei which remain within corresponding to the yolk-nuclei of other Arthropod eggs. In the fact that the yolk itself remains segmented these forms are peculiar.

As the segmentation of the yolk gradually disappears, the blastoderm divides into an outer and an inner layer of cells (METSCHNIKOFF, Fig. 15 *C*). About this time, large clear bodies appear between the blastoderm and the egg-integument; these contain structures resembling nuclei, and therefore resemble cells (Fig. 15 *C*). METSCHNIKOFF was reminded by them of an embryonic envelope, but could not convince himself that such a covering was actually present, and regarded these structures as disintegrated masses of albumen, a view also taken by STECKER. These cells recall those found beneath the cuticular envelopes in the Mites (CLAPARÈDE's haemamoebae, Fig. 53, p. 99).

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* We have not heard of any more detailed work on this subject by BARROIS; STECKER's preliminary notice also seems not to have been followed by any larger treatise. [See BARROIS (App. to Lit. on Pseudoscorpiones, No. I.).—ED.]

† [BARROIS (App. to Lit. on Pseudoscorpiones, No. I.) has recently very fully investigated the development of *Chelifer*; he finds that segmentation may be either total or partial, the latter condition predominating and resulting in a core of yolk with peripheral cells, some large, which form the blastoderm, others very small, which become applied to the vitelline membrane. A deep median ventral longitudinal groove appears, from the walls of which mesoderm-cells are proliferated off. Origin of the entoderm obscure, nuclei appear in the yolk.—ED.]

The further differentiation of the embryo is characterised by the early and pronounced development of the future anterior end of the body; this appears as a great accumulation of cells belonging to the inner layer of the blastoderm. A pair of marked swellings appear on either side of this region, and from each of these a large truncated appendage soon arises (Fig. 16 *A*). These processes are the rudiments of the pedipalps which are here, as in *Scorpio*, the first limbs to appear. They are still in a very primitive condition, the inner yolk-mass extending far into them (Fig. 16 *A* and *B*). In front of the limbs, towards the ventral surface, there is a swelling which, even at this early stage, is distinguished by its strong musculature, and consequently has a striped appearance (Figs. 16 *A* and *B*, *r*, 17 *A*). This is the rudiment of a provisional organ—a kind of sucking proboscis (Fig. 16 *C*) which serves for attachment and for taking in food. The embryo leaves the egg at this stage, having previously undergone a larval ecdysis. A fine cuticle, which occupies a peculiar position between the bases of the two limbs, becomes detached from the embryo. The larva, when hatched, at the youngest stage shown in Fig. 16 *A*, has the muscular proboscis, the truncated pedipalps, and the rudiment of the abdomen directed forward. The proboscis, which is regarded as a modified upper lip, already seems to function as a sucker, for the larva attaches itself by means of this organ to the ventral surface of the mother. The proboscis lengthens considerably at a later stage, and becomes applied to the ventral surface of the larva, lying between the limbs (Fig. 16 *B*). Barrois has described a provisional *oral* aperture situated between the pedipalps. There are also, according to Barrois,

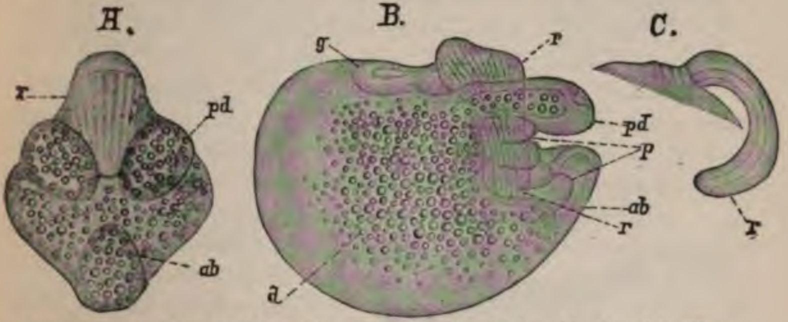

Fig. 16.—*A* and *B*, larva of *Chelifer*; *C*, provisional proboscis of an older stage (after Metschnikoff). *A*, ventral aspect; *B* and *C*, from the side. *ab*, abdomen; *d*, yolk; *g*, brain; *p*, the four limbs; *pd*, pedipalps; *r*, proboscis (provisional larval organ).

chitinous structures in the proboscis. There is no mention of an external aperture to the proboscis; **Metschnikoff** could not find one, although he assumes that the larva obtains its nourishment by sucking the blood of the mother. Soon after becoming attached to the body of the mother, it swells considerably, and becomes filled with a clear fluid (*cf.* Fig. 17 *A* and *B*). If this fluid comes from outside, we must certainly assume that an intestinal epithelium has already developed round the inner yolk-mass, although no such differentiation has been recognised.

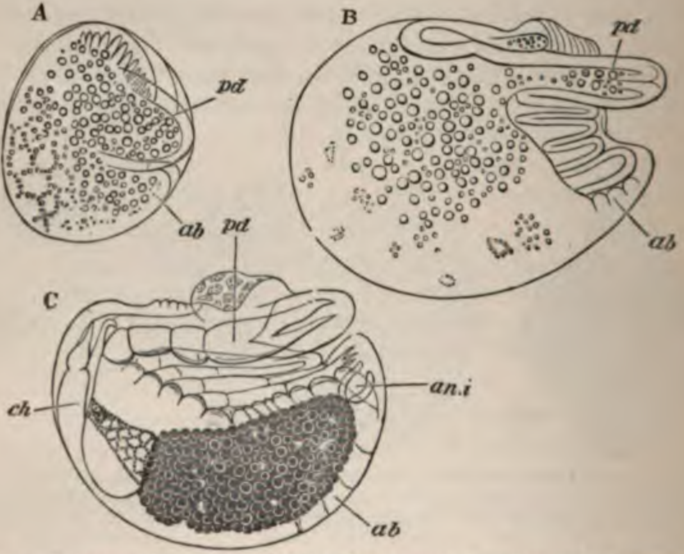

Fig. 17.—Embryo and larvae of *Chelifer* (after **Metschnikoff**, from **Balfour**). *A*, embryo in the egg-integument; *B* and *C*, larvae taken from the ventral surface of the mother. *ab*, abdomen with the provisional appendages; *an.i*, anal invagination; *ch*, chelicerae; *pd*, pedipalps; between the last two (*ch* and *pd*) the upper lip is visible in *C*. Above the pedipalps are seen, in *A* the rudiment, in *B* the base, and in *C* the last vestige of the proboscis. In *B* the rudiment of the oesophageal ganglion can be recognised, lying dorsally to the proboscis. The pedipalps are followed posteriorly by the four limbs, and, in *B*, by the rudimentary abdominal appendages. *C* represents the larva just undergoing ecdysis. The larval integument is partly loosened (noticeably on the ventral side); the remains of the proboscis are attached to it.

The later stages (Figs. 16 and 17 *B*) differ from the youngest larvae (Fig. 16 *A*) in external form chiefly in the swollen nature of the dorsal region, brought about by the presence of the clear fluid mentioned above. Other modifications have also taken place, the rudiments of the first pair of limbs having budded out behind the pedipalps, and these are followed by the three other pairs

(Fig. 17 *B*). On the abdomen, which is bent ventrally, four pairs of limb-rudiments appear (Fig. 17 *B*), which, however, soon completely degenerate. The *Pseudoscorpiones* agree in this respect with other Arachnida. The most anterior pair of limbs is still wanting, but a paired thickening is found dorsally, above the base of the proboscis; this has apparently arisen from an invagination, and is the rudiment of the supra-oesophageal ganglion (Fig. 16 *B*, *g*). This recalls the cephalic pits of the Scorpiones and Araneae (pp. 12, 53).

The larva continues to approach the adult in form, segmentation appearing both in the limbs and in the abdomen, but the cephalothorax remains unsegmented. The chelicerae have, in the meantime, appeared in front of the pedipalps. The true upper lip arises between them, some way from and altogether independent of the larval proboscis (Fig. 17 *C*). The proboscis degenerates, the last vestige of it being lost when the larva moults, at the stage depicted in Fig. 17 *C*. It is then still found attached by a delicate thread to a point behind the future mouth, until it is cast off with the larval integument (Barrois). A large mass of yolk can still be seen within the body, enclosed in the enteron, which opens externally through the proctodaeum at the posterior end of the body (Fig. 17 *C*, *an.i*). The oesophagus is probably also formed by an ectodermal invagination (Metschnikoff).

General Considerations. The ontogeny of the Pseudoscorpiones is remarkable on account of the embryo leaving the egg-membrane with a much simpler structure and at a much earlier stage than in other Arachnida. Further, the larvae, in their half parasitic life on the body of the mother, have developed a provisional sucking organ which at first lies in front of the first pair of limbs, but shifts back later, in consequence of processes of growth, on to the ventral surface (Figs. 16 and 17); this organ, however, cannot be compared to a pair of limbs. No homologue has so far been discovered among the Arachnida for this proboscis, which must therefore be regarded as an organ acquired by the Pseudoscorpiones through their peculiar method of development.

The difference between the ontogeny of the Pseudoscorpiones and that of the Scorpiones, to which they are perhaps most nearly related, is very striking. The cleavage, the formation of the blastoderm, and the first rudiment of the embryo in the two forms can hardly be compared. They also differ in important points of their organisation. The absence of the tail-like abdomen, the disappearance of the abdominal ganglia (Croneberg), the position of the genital apertures (in the second abdominal segment), and, not least, their tracheal respiration, remove the *Chernetidae* from the true Scorpiones so far that the variations in their method of development appear comparatively unimportant. Attempts have been made to connect the Pseudoscorpiones with other divisions of the Arachnida, especially with the Opiliones, but these have not been sufficiently based on the organisation of the two groups. We must therefore, according to a recent investigator of the anatomy of the *Chernetidae* (CRONEBERG), leave the systematic position of the Pseudoscorpiones undecided, since their ontogeny, so far as it is yet known, throws no light upon the subject.

IV. Opiliones.

The spherical eggs of the Opiliones are surrounded by two membranes. The inner membrane is secreted by the egg, the outer by the epithelium of the genital duct; they represent the vitelline membrane and the chorion. The eggs, glued together so as to form a large ball, are deposited in a hole in the ground (HENKING). The first ontogenetic processes have been closely studied in *Opilio* and *Leiobunum*, by HENKING, but we are unable to accept his view of the origin of the cleavage-nuclei through free nuclear formation, since it contradicts what is known of other Arthropoda.* According to FAUSSEK, the egg of *Phalangium* divides up into a number of large spherical cells filled with yolk-spherules, each cell containing a central nucleus. Cleavage is therefore total. These cells might be compared to the yolk-pyramids in the eggs of the Araneae, but, in the subsequent processes, these cells in the Opiliones seem to differ from those structures. A cleavage-cavity does not appear. The formation of the blastoderm occurs by the separation and more rapid division of some of the peripheral cells. Not all the cells, indeed, not even the majority of them, rise to the surface to form the blastoderm, a large proportion of them remain within the egg as yolk-cells (HENKING, FAUSSEK). The formation of the blastoderm takes place more rapidly in one half of the egg than in the other, a condition similar to that observed in the Araneae.

Active increase in number of the blastomeres in one region of the blastoderm leads to the formation of a thickening in it; this is the germ-disc. According to FAUSSEK, immigration of cells into the yolk-mass from the disc does not take place; the entoderm being possibly represented by the cells which remain in the yolk, and from them, at a later stage, the epithelium of the enteron arises.

The origin of the entoderm from cells which, from the first, remain behind in the yolk, has been assumed for the Araneae (SCHIMKEWITSCH), but the formation of the germ-layers in the Opiliones has not yet been observed sufficiently

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* [Most cytologists do not believe in the existence of the process termed free nuclear formation; all modern research tends to prove that every nucleus has originated directly from a pre-existing one.—ED.]

closely for us to decide whether this is also the case in them. **Faussek** found in embryos in which the segmentation of the germ-band is commencing, an accumulation of cells at the posterior end of the band, which strongly resembles the point of ingrowth in the germ-band of the Scorpiones. The statements hitherto made as to the nature of this structure are, however, so contradictory that it is impossible to gain any clear idea of it. **Faussek** derives these cells, which appear like a thickening of the blastoderm, from a deposit of yolk-cells on the blastoderm. At first he derived the genital glands from this deposit, *i.e.*, from yolk-cells, but he afterwards traced them to a thickening of the blastoderm which appeared at a very early stage. A more exact account of the partly contradictory statements on this subject may be expected in **Faussek**'s larger work [App. to Lit. on Opiliones, Nos. III. and IV.]

The mesoderm, so far as we can gather from the few statements on the subject, splits into a somatic and a splanchnic layer, so that in this respect also there is resemblance with the Scorpiones and the Araneae.

The enteron seems to form as in the Araneae, apart from the origin of the entoderm, which arises differently according to **Faussek**. The yolk is directly surrounded by the splanchnic layer of the mesoderm, and the yolk-cells now become applied to this layer, eventually giving rise to the continuous epithelium of the enteron. This process commences in the anterior part of the body.

We have only a few isolated statements as to the further development of the Opiliones. **Metschnikoff** (No. 34, p. 520) traces the origin of the abdominal limbs, and **Balbiani** describes a few of the later ontogenetic stages. It appears that the cephalo-thoracic segments to which the four pairs of limbs belong are distinctly marked off from one another in the embryo, but this segmentation disappears during the further course of development, and is not recognisable in the adult. Between the eyes and the bases of the chelicerae lies an unpaired, spine-like structure, which, like similar structures in the Araneae, and especially in the Myriopoda (Chilognatha), we shall call the *egg-tooth* (p. 58, and cf. the chapter on the Myriopoda).

The little that is known of the ontogeny of the Opiliones is in harmony with that of the Arachnida generally. An important feature which is still recognisable in the adult, seems, according to **Balbiani**, to be very marked in the embryo. This is the occurrence of masticatory ridges on the pedipalps and on the two anterior pairs of limbs. Herein we find a striking resemblance to the Scorpiones. The Opiliones further resemble other Arachnida in the number and position of the limbs, and in the presence of a coxal gland (**MacLeod**), homologous with the synonymous organ in other Arachnids. Whereas, however, in other groups, this gland is merely provisional, and degenerates in the adult (Scorpiones, Araneae), in the Opiliones it is a well-developed organ, still functional in the adult, and consisting of a large coiled canal, a wide, sac-like reservoir, and an efferent duct; the latter opening externally at the base of the third ambulatory limb (Loman, No. 9).[*]

V. **Solifugae.**[†]

Of the ontogeny of the *Solifugae*, like that of all the Arachnida already considered, so far as we are aware, very little is known. The little that we do know is in connection with ***Galeodes araneoides***, some of the later ontogenetic stages of which have been described by Croneberg.[‡]

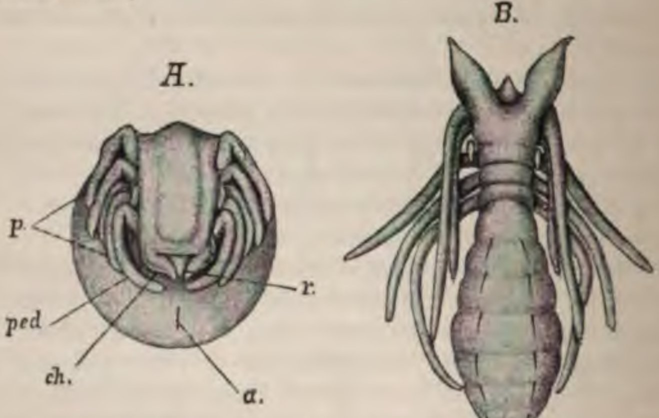

Fig. 18.—*A*, embryo, and *B*, newly-hatched young form of *Galeodes araneoides* (after Croneberg). *a*, anus; *ch*, chelicerae; *ped*, pedipalps; *p*, limbs; *r*, rostrum.

The first embryo discovered by Croneberg was already in an advanced stage, not far from hatching. In Fig. 18, *A*, it is seen to be very like the embryo of an Araneid. As in the latter, the spherical abdomen, probably well filled with yolk, forms the chief

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[*] [Lebedinsky (App. to Lit. on Opiliones, No. V.) describes this gland in *Phalangium opilio* as arising entirely from the mesoderm, the ectoderm only sharing in the formation of the external aperture. He expresses his belief that the coxal glands of Arachnids, the antennae, shell, and coxal glands of Crustacea and *Limulus*, are all nephridia and thoroughly homodynamic, but perhaps not thoroughly homologous, some being derived from the primary and others from the secondary coelom. See also, Faussek (App. to Lit. on Opiliones, No. IV).—Ed.]

[†] [See Bernard, App. to Lit. on Solifugae. No. I.]

[‡] [Birula (App. to Lit. on Solifugae, No. II.) finds that the ova of *Galeodes* develop within the cavities of the ovaries; there are no embryonic membranes; the thoracic and abdominal segments are visible before the appendages. A flexure-reversal occurs as in the Araneae. Hutton states that the Solifugae are oviparous.—Ed.]

part of the body. The broad and flattened cephalo-thorax seems closely pressed against the ventral surface of the abdomen. The rudiments of the limbs are seen on the cephalo-thorax; the chelicerae are bent towards the rostrum (Fig. 18, *A*), the latter being approximated to the slit-like anal aperture.

After the embryo is hatched, the abdomen appears longer, and shows a few slight constrictions, which no doubt correspond to segments (Fig. 18, *B*). It carries two rows of dorsal setae, six in each row. These are the only traces of the hairy covering which is so profuse in the adult. The chitinous integument of the young is thus only provisional. The young probably remain for some time after hatching in a pupa-like condition, resembling in this respect the Araneae (p. 58), which after leaving the egg remain quiescent surrounded by a cuticular envelope, which is not cast off for some time. This fact explains why the limbs (now bent backwards) up to this time show no traces of segmentation (Fig. 18, *B*, CRONEBERG), and are also devoid of claws. No abdominal limbs were found in the young animal, nor was their presence to be expected at so late a stage.

A very remarkable structure, not occurring in the adult,* is a pair of wing-like appendages, which arise dorsally between the points of insertion of the first and second pairs of limbs. These outgrowths consist of a double layer of cells, invested with a cuticle, and thus represent integumental folds; no nerves or tracheae extend into them, and they are also devoid of muscles.

The significance of these wing-like appendages is not understood. CRONEBERG compares them to the paired appendages of the *Asellus* embryo (Vol. ii., p. 151), which are to be regarded as vestiges of the shell, but lays no special stress on this comparison.†

The *Solifugae* are distinguished from the other Arachnida by a few important features, in which they seem more nearly to approach the Insecta. The most anterior pair of limbs with the segment to which it belongs enters into close relation with the preceding (cephalic) segments, and is marked off from the posterior (thoracic) segments, so that a separate cephalic region with three pairs of limbs arises. This has been compared to the head of the Insecta and the next region, which now consists only of three segments, each with a pair of limbs, to the thorax of the Insecta. The resemblance is increased

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* CRONEBERG examined adults of the same species, and found that this structure was altogether wanting in them.

† [It is now generally agreed that these structures are embryonic sensory organs, and similar to those found in *Phrynus*. See BRUCE (Lit. on Pedipalpi, 26) and LAURIE (App. to Lit. on Pedipalpi, No. I.).—ED.]

by the fact that the abdomen consists of ten segments visible externally. It is a striking fact that the *Solifugae*, which breathe by means of dendriform tracheae, possess at least three pairs of stigmata; the first opens on the fourth segment of the body, viz., the second thoracic (*i.e.*, the first free thoracic) segment; the second pair opens on the second abdominal, and the third pair, which are closely approximated, open on the third abdominal segment. A fourth opening may be present as a median stigma on the fourth abdominal somite.*

We cannot agree with those who find actual relationship to the Insecta implied in the very striking features we have mentioned, and regard the *Solifugae* as a connecting link between the two stocks of air-breathing Arthropoda. The value of a division of the anterior body into head and thorax, in which the three anterior pairs of limbs would have to be considered as the equivalents of the three pairs of oral limbs in the Insecta, is diminished by the fact that one pair is still wanting, *i.e.*, there is in the *Solifugae* no homologue for the antennae of the Insecta. The most difficult point to explain is the position of the pair of stigmata on the cephalo-thorax; we can only assume that it was acquired later. The assumption gains in probability when we find that stigmata appear on the cephalo-thorax in the Acarina also, on the legs in Opiliones (HANSEN), and on the head in *Scolopendrella* and *Sminthurus* (?). The presence of a spiral filament in the tracheae of the *Solifugae* is no proof of their relationship to the Insecta, since it occurs also in other Arachnida.

In spite of the external division of the body into three parts, the *Solifugae* agree so closely with the Arachnida in outer and inner organisation, that we are not justified in separating them from that class. The shape of the chelicerae, the possession of a coxal gland, like that which is found in the Arachnida (MACLEOD, No. 44), the hepatic tubules derived from the enteron,† the position of the genital aperture on the first abdominal segment, and other less striking features favour the Arachnid character of the *Solifugae*. We therefore regard them as a branch of the Arachnid stock developed in a special direction, a view which corresponds to that of RAY LANKESTER (No. 45) and other writers on this subject. The slight

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* [BERNARD, *op. cit.*]

† With regard to the liver, it should be mentioned that a more recent observer (BIRULA, No. 42) has found certain differences in structure between this organ in the Solifugae and the Arachnida in general. He also, however, describes the liver as a well-developed organ filling up the interstices between the other organs, a description which applies to the liver of an *Arachnid*, but not to that of an Insect.

data that are afforded by ontogeny confirm our view, the embryo of *Galeodes* closely resembling an Araneid embryo. More accurate data as to the development of the *Solifugae* are very desirable.

VI. Araneae.*

Systematic :

A. TETRAPNEUMONES.

Avicularia (*Mygale*), *Atypus*.

B. DIPNEUMONES.

Epeira, *Theridium*, *Agalena*, *Lycosa*, and all the other Araneae mentioned.

Oviposition and the Constitution of the Egg. The Araneae build nests or prepare cocoons for their eggs, and usually watch over them. In many cases the cocoons are carried about by the mother, held by the chelicerae (*e.g.*, *Dolomedes*, *Pisaura*) or attached to the abdomen (*e.g.*, *Lycosa*, *Tarantula*).

The eggs, which are rich in yolk, are surrounded by a vitelline membrane as well as by an external envelope, probably secreted by the oviduct, the latter being described as the chorion. A thin protoplasmic layer (the periplasm or blastem) covers the yolk, which in turn surrounds a central mass of protoplasm (the centroplasm), within which the nucleus is situated; from this central mass fine protoplasmic strands extend to the surface, thus breaking up the yolk into columns.

Besides the nucleus, a remarkable structure is found in the eggs of Araneae, and called the yolk-nucleus, but this is not yet sufficiently understood. It consists of a compact accumulation of spherules; occasionally it is quite a complicated structure, composed of several concentric layers. When the egg matures the yolk-nucleus usually disappears, but it appears sometimes to be still retained, and is said to be still found near the nucleus in one of the yolk-complexes in the two- and four-celled stages of cleavage (KISHINOUYE).

According to LUDWIG (No. 66), the external envelope is marked out into polygonal areas, but this has recently been referred to the breaking up of the periplasm into polygonal divisions, SABATIER (No. 70) and LOCY (No. 64), these writers thus agreeing with older statements made by BALBIANI (No. 46). This polygonal marking must not be confounded with blastoderm-formation (which only occurs later); the former is said to appear even before cleavage

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* [POCOCK divides the Araneae into two groups—
A. Mesothelae, comprising one genus, viz., *Liphistius*, with a segmented abdomen.
B. Opisthothelae { Mygalomorphae.
Arachnomorphae.—ED.]

takes place. LOCY, with whom KISHINOUYE agrees in the main, explains these markings by contractions of the egg after it is laid, drawing the periplasm closer to the yolk. The columns of yolk-granules can be separately recognised at the periphery as prominences, and this causes the polygonal markings on the surface. Some of BALBIANI's numerous figures that bear on this point seem to confirm this view, while others contradict it. In these figures, besides the original division of the periplasm into areas, another and true division is shown, caused by the presence of blastoderm cells. Since the egg is said to contract, there might be a regular folding of the vitelline membrane (in the form of polygonal areas), such as is said to occur in *Cetochilus* (GROBBEN), but this possibility seems to be excluded, as LOCY mentions a perivitelline fluid which appears when the egg contracts, between its surface and the vitelline membrane.

1. Cleavage and Formation of Germ-Layers.

Cleavage may here at first be described as total, but passes later into a superficial form. The central nucleus divides, the two daughter nuclei still lying near the centre of the egg (Fig. 21 *A*).

FIG. 19.—Three ontogenetic stages of *Philodromus limbatus* (after H. LUDWIG, from BALFOUR's *Text-book*).

Although there is no furrow dividing the egg into two, a complete division is indicated, at first, however, only in the yolk. The yolk-granules become arranged radially one behind another in the form of cylindrical columns (LUDWIG, Figs. 19 and 21 *A*). These columns, radiating from the centre, become divided into two groups by the division of the nucleus into two (Fig. 19 *B*). Between them lies formative yolk. As nuclear division proceeds, the two groups of columns, which LUDWIG described as rosettes, again divide, and yield four rosettes (Fig. 19 *C*), which then divide further into eight, sixteen, and thirty-two rosettes, following the usual course of total and equal cleavage. Each rosette, which has now become a simple column, has a nucleus. In the further course of cleavage (Fig. 20 *A*) the nuclei shift to the periphery, accompanied by the formative protoplasm belonging to them. These, together with the periplasm already present, separate from the yolk to form a peripheral layer, which now contains the nuclei, and must thus be described as the blastoderm (Fig. 20 *B*, *bl*). The yolk-columns, or rather pyramids, may still be present at this time. Even earlier a cavity appears at the centre, the cleavage-cavity (Fig. 20, *B*), the central yolk-mass being withdrawn into the blastomeres as they develop, and pressing further towards the periphery.

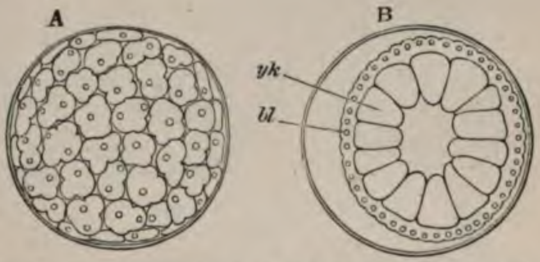

Fig. 20.—Superficial aspect and optical section of a later stage in the cleavage of *Philodromus limbatus* (after Ludwig, from Balfour's *Text-book*). *bl*, blastoderm; *yk*, yolk-pyramids. In the space between the vitelline membrane and the blastoderm the perivitelline fluid is found (*B*).

The yolk-rosettes do not seem, as a rule, to be so distinct as Ludwig found them in *Philodromus*. Yolk-pyramids have also been seen in *Agalena*, *Theridium*, *Epeira*, *Pholcus*, and other forms, but the groups formed by them (the rosettes of *Philodromus*) lie closer to one another (Fig. 21 *A*). A stage in which there are eight such groups closely resembles an egg that has undergone total and equal cleavage, and that has a small cleavage-cavity (Fig. 21 *B*). Each group of yolk-columns with its nucleus corresponds to a blastomere. The blastomeres here also divide further, as in a case of equal cleavage, and when, after repeated division, a large number of blastomeres (about 128) have been formed, the nuclei, which have meantime shifted to the periphery, with their protoplasm, separate from the yolk below them, and thus give rise to the blastoderm (Fig. 21 *C* and *D*). The cleavage-cavity, which may be fairly large (Figs. 20 *B* and 21 *C*), becomes again filled with yolk, and the regular arrangement of the latter is gradually lost (Fig. 21 *D* and *E*). The formation of the blastoderm seems to take place more rapidly in the one half of the egg than in the other (Fig. 21 *E*), (Salensky, Ludwig, Locy, Morin, Schimkewitsch). The former is the region in which the germ-band appears later, and may possibly correspond with the germ-disc from which the blastoderm spreads in *Scorpio.*

The method of cleavage of the Araneid egg agrees closely with that of Crustacean eggs classed under type II. (Vol. ii., p. 109). If, as appears probable to us, a cleavage-cavity does not occur in all Araneid eggs, the centre in some cases remaining filled with an unsegmented mass of yolk, these latter cases would probably be referable to that type which was described, in connection with the Crustacea, as total cleavage with subsequent transition to superficial cleavage.

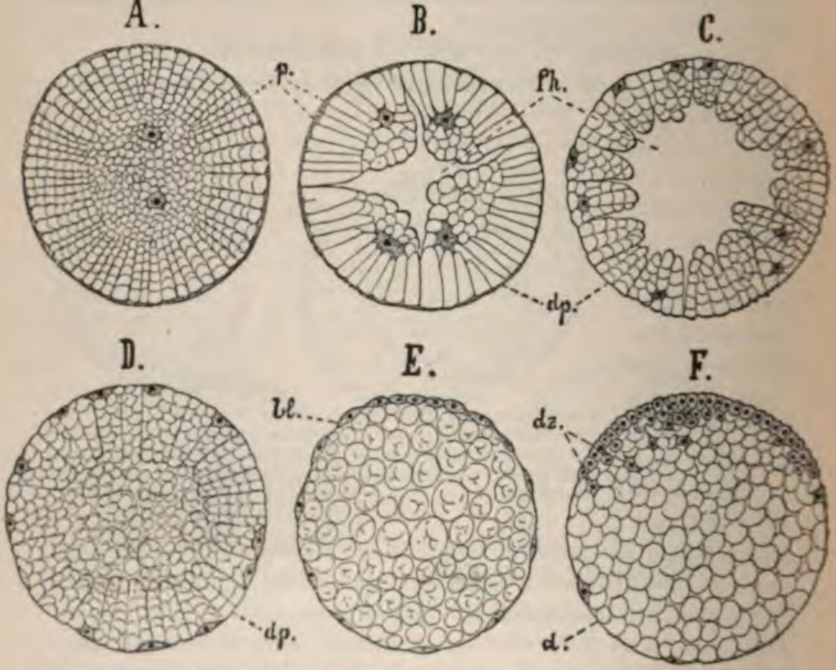

FIG. 21.—Sections through the egg of *Theridium maculatum* in different stages of cleavage and blastoderm-formation (after MORIN). *bl*, blastoderm; *d*, yolk; *dp*, yolk-pyramids; *dz*, yolk-cells; *fh*, cleavage-cavity; *p*, periplasm.

[The blastomeres are, for the most part, flattened (Fig. 21 *E*), but at one spot the cells become spherical and multiply rapidly, consequently a large accumulation of blastoderm-cells, several deep, forms at this spot. By reflected light this spot appears as a round whitish area. Shortly after this a second thickening, and consequently a second white area, appears. These two thickenings herald the formation of the germ-disc.]

There is little agreement among authors concerning the ontogenetic processes which follow the formation of the blastoderm, some ascribing great significance to the prominence, called by **Claparède** the *primitive cumulus*, which appears in the blastoderm by the thickening of the cell-layer * (Figs. 22 *B* and 23 *A* and *B*), others denying its importance. According to **Morin**, a thickening of the blastoderm arises in the region which corresponds to the later ventral surface, *i.e.*, to the rudiment of the germ-band (Fig. 21 *F*); not only do the cells here increase in size, but some of them separate from the blastoderm, and form definite layers; the blastoderm thus becomes multilaminar. At the same time a few cells in this region become entirely disconnected from the rest, and migrate into the yolk (Fig. 21 *F*, *dz*). The *three germ-layers* may be now recognised. An outer layer, which constitutes the greater part of the blastoderm, is the ectoderm. Below this, at one pole of the egg, is the mesoderm, while the cells which have migrated into the yolk represent the entoderm. In the Araneids observed by **Morin**, the primitive cumulus arose only after the germ-layers had formed, if indeed it arose at all. It was wanting in *Theridium*, the form in which the origin of the germ-layers has been just

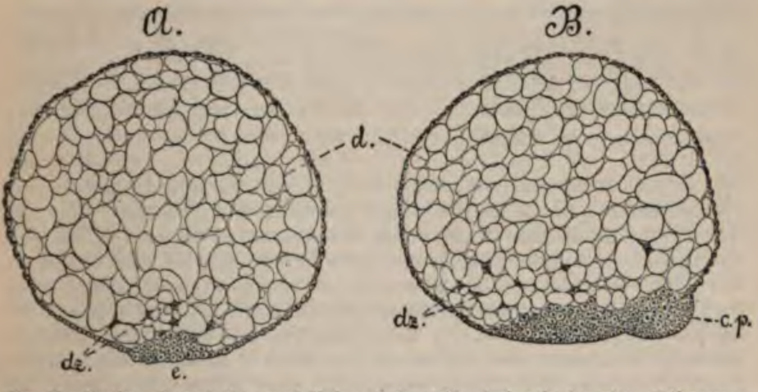

Fig. 22.—Sections through the egg of *Pholcus phalangioides* during the formation of the germ-layers (after **Morin**). *c.p.* primitive cumulus; *d*, yolk; *dz*, yolk-cells; *e*, point of ingrowth.

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* [Unfortunately there is a good deal of confusion surrounding the term "primitive cumulus." As stated above, there are two thickened white areas in the blastoderm; and according to **Kishinouye**, **Claparède** overlooked the first of these, and applied the term "primitive cumulus" to the second. The former author terms them the primary and secondary thickenings; but **Kingsley**, while agreeing that **Kishinouye** may be right, nevertheless retains **Claparède**'s term "primitive cumulus" for the first thickening.—Ed.]

described. It is, however, not impossible that those cases in which it is wanting are not primitive, but are specialised, and that it really is of greater importance than its late appearance in *Pholcus* and its entire absence in *Theridium* would lead us to believe. This last view is confirmed by the recently-published work of KISHINOUYE (p. 44).

The primitive cumulus* arises as a thickening of the blastoderm (Fig. 22 *B*), and may project from it as a prominence of considerable size (*e.g.*, in *Tegenaria* and *Agalena*, Fig. 23, *A* and *B*, p. 46). It has been found in most of the Araneae as yet examined. A depression is said to appear in front of it (SALENSKY, No. 71, SCHIMKEWITSCH, No. 72). We are tempted to regard the latter as the blastopore, at the posterior edge of which the ingrowth of cells is specially active, as in the Scorpiones (p. 2). Some of the statements as to the relation of the primitive cumulus to the germ-layers in the process of formation (*e.g.*, those of BRUCE, No. 54, and LENDL, No. 63) must evidently be understood in this way.

If we consider the primitive cumulus to lie at the posterior end of the embryo, we find ourselves in the position which was taken up by BALFOUR (No. 47). Although, since the time of this writer, the ontogeny of the Araneae has been investigated by several zoologists, very little further light has been thrown on this point. According to the above view, the primitive cumulus corresponded more or less to the future caudal end, the depression lying in front of it, and the cephalic lobes again in front of this (BALFOUR, SCHIMKEWITSCH, LENDL); according to another view, the caudal end arises at some distance from the primitive cumulus, the cephalic lobes lying nearer it (BALBIANI, LOCY). In inclining rather to the view that the primitive cumulus corresponds to the posterior end of the embryo, we are actuated chiefly by theoretical considerations. The figures given by MORIN and SCHIMKEWITSCH seem also to support such a conclusion. It is, however, true that there is little convincing evidence for our assumption that the mesoderm arises from the primitive cumulus. There is, indeed, evidence of active proliferation of cells in the primitive cumulus, but in front of it also (in the region of the future germ-band) the blastoderm appears to be multilaminar (Fig. 22 *B*). It has already been mentioned that MORIN entirely denies this significance of the cumulus. According to him, when such a prominence appears, it arises only after the development of the germ-layers. It cannot, however, be denied that MORIN himself represents it as of considerable size (Fig. 22 *B*). It decreases later by giving off isolated mesoderm cells, and, by degrees, shifts dorsally. This displacement is also evident in CLAPARÈDE'S figures, if indeed the prominence seen in them actually corresponds to the primitive cumulus (Fig. 25 *A* and *B*, p. 48). That the blastopore, or the last

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* [The authors here use this term in the sense in which it was originally applied by CLAPARÈDE, *i.e.*, they apply it to the thickening which forms a projection from the surface of the blastoderm, which KISHINOUYE termed the secondary thickening. KINGSLEY, on the other hand, terms the primary thickening in *Limulus* the primitive cumulus.—ED.]

traces of it, should occupy such a position is from previous evidence improbable, unless we may assume that the proliferating area shifted as the posterior end developed, and thus attained a position which is apparently dorsal. Further discussion of this point is unadvisable, as a glance at the figures of CLAPARÈDE, BALBIANI, SALENSKY, BALFOUR, SCHIMKEWITSCH, LOCY, and MORIN shows that they cannot be brought into agreement with one another. It is evident that the difficulty which attends investigation of this point is the cause of our uncertainty with regard to it. Orientation in the almost spherical egg is rendered still more difficult by the appearance of the different parts of the embryo (cephalic lobes and caudal end) simultaneously with the degeneration of the primitive cumulus. On this account one of the more recent investigators of the ontogeny of the Araneae, KISHINOUYE, was unable satisfactorily to decide the position of the primitive cumulus in the embryo. We must, for the present, accept with some hesitation the view that the depression which appears in the blastoderm of the Araneae and the primitive cumulus corresponds to gastrulation, although such an interpretation appears very probable, especially when comparison is made with the Scorpiones.

This subject is not exhausted with the question as to whether the germ-layers originate in a region corresponding to the later ventral surface, in which the primitive cumulus represents an area of active cell-proliferation (perhaps a point of ingrowth), for there exists a different interpretation of the origin of the germ-layer. According to the view given above, it is to be assumed that the cleavage-cells shift to the periphery to form the blastoderm, and that the germ-layers originate there by an ingrowth of cells (Figs. 21, *F*, and 22, *A* and *B*). While the mesoderm remains as a compact accumulation on the ventral side, the cells of the entoderm become detached from it and shift into the yolk; from these the enteron forms later. The origin and the fate of these yolk-cells is otherwise described by BALFOUR, SCHIMKEWITSCH, LOCY (?). The most important point in these diverging views is the assumption that some of the cleavage-cells remain in the yolk. These cells, which are not utilised in the formation of the blastoderm, do not represent the entoderm alone, but some of them give rise to mesoderm-elements (BALFOUR, SCHIMKEWITSCH).

According to SCHIMKEWITSCH, cleavage and the formation of the blastoderm take place in such a way that the egg breaks up into a large number of yolk-pyramids in the manner already described. Each of these pyramids contains a nucleus which at first lies at the centre. The nuclei shift to the periphery later, and there, with the protoplasm which surrounds them, become separated from the yolk. An outer cell-layer, the blastoderm, is thus formed. It appears, however, as if a further division of the nuclei had taken place previously, and a *large number of nuclei had remained within the yolk*; at least, this is what we understand from SCHIMKEWITSCH's description of the cleavage-process.* During the development of the blastoderm there is a further increase in the number of the nuclei which remained within the yolk. Before following its further fate, we must mention a process which was observed by SCHIMKEWITSCH in Araneid eggs, and had been previously noticed by SALENSKY. The blastoderm-cells which at first surround the egg, shift towards the ventral side, and there

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* The statements of SCHIMKEWITSCH as to the breaking up of the yolk-pyramids and the formation of uninuclear and multinuclear yolk-cells do not come within our scope, and also require corroboration. As a whole, his figures agree with the descriptions of earlier writers. SCHIMKEWITSCH also found the central cleavage-cavity in a few forms (*Tegenaria*, *Epeira*), and describes it as filled with masses of yolk, in the way described for *Theridium* (Fig. 21, *C* and *D*).

form a thickening which, together with the later proliferation of cells at this spot, yields the rudiment of the germ-band. Morin's account also, as far as we can follow it, seems to confirm this, and the figures adopted from him (Fig. 21 *D–F*) show that an accumulation of blastoderm-cells at first lies on the dorsal side of the egg, while at a later stage only a few cells are perceptible in this region. According to Schimkewitsch, the dorsal side of the egg becomes completely denuded of blastoderm, which only later grows out towards it again. We were at first disposed to attribute the absence of blastoderm on the dorsal side rather to a belated advance of the nuclei out of the yolk, especially as authors state that the formation of the blastoderm progresses from the ventral to the dorsal side. There seemed here to be a distant resemblance to the cleavage and the formation of the blastoderm as observed in the eggs of *Scorpio*. Further investigation is needed to show whether this conjecture is correct, or whether such a marked redistribution of the blastoderm-cells as is shown in the figures actually takes place. A similar crowding together of the blastoderm-cells, though not nearly to such a great extent, has also been observed in other Arthropoda (*Astacus*, *cf.* Vol. ii., p. 128).

According to Schimkewitsch, who on this point is essentially in accord with Balfour, the yolk-cells take part to no inconsiderable extent in the formation of the mesoderm, although the chief mass of them is to be described as entodermic. Schimkewitsch, like Balfour, assumes a two-fold origin for the mesoderm, inasmuch as it is formed from the thickening of the ventrally situated blastoderm, especially from the primitive cumulus, and also by the addition of yolk-cells to this thickened region. Certain modifications here appear in individual forms (*Tegenaria*, *Epeira*, *Lycosa*); upon these, however, we shall not enter, as we are unable to agree with this view. Of the two opposed views, the one assuming the existence of yolk-cells giving origin to the entoderm and the mesoderm to some extent, the other deriving both the entoderm and the mesoderm from the blastoderm by a process comparable to gastrulation, the latter appears to us to be by far the more justifiable. This view is confirmed by Kishinouye's recent work (No. 62). This observer found no nuclei in the yolk after the formation of the blastoderm, but observed cells migrating into the yolk from the blastodermic thickening (Figs. 21 and 22). These cells, which become distributed through the yolk, form the entoderm. Further thickening of the ventral region of the blastoderm gives rise to the mesoderm, as was described above (p. 41). The ventral blastodermic thickening known to us as the primitive cumulus is in any case of significance in connection with the formation of these two germ-layers, for it, like the ventral plate (to be described later), appears before the differentiation of the germ-layers (Kishinouye), and not after it, as Morin assumed (p. 41).

When we trace back the *formation of the germ-layers* to the blastoderm, we thereby imply that the yolk-cells also arise from the blastoderm. These latter, according to the unanimous opinion of authors, contain, in the Araneae, the rudiments of the whole entoderm, giving rise later to the epithelium of the enteron. If these cells were to remain in the yolk when cleavage takes place, the process of blastoderm-formation would have to be regarded as epibolic, but this is contradicted by what occurs in related forms. The germ-layers are moreover formed in the Scorpiones also by the ingrowth of cells on the ventral side of the blastoderm, and the entoderm, when first appearing, occupies this position in both these divisions of the Arachnida. In the Scorpiones, it forms a regular epithelium, so that it cannot fail to be recognised as a separate germ-layer, but here also isolated cells enter the yolk. All these facts confirm us in regarding the view of the formation of the germ-layers adopted by MORIN and KISHINOUYE (Fig. 21 *F*) as correct. It cannot, however, be denied that the figures given by SCHIMKEWITSCH, and especially those given by BALFOUR, show yolk-cells in earlier stages and further removed from the thickened part of the blastoderm, which might rather be assumed to have remained behind in the yolk at the time of cleavage, than to have become detached from the thickened part of the blastoderm. If this should be the case, the view here taken is not thereby contradicted; we have then to do merely with single cells which were not utilised in the formation of the blastoderm, and remained behind in the yolk. These cells, as *vitellophags*, perhaps render the absorption of the yolk possible. In that case we must assume that they do not later enter into the formation of the entoderm, but probably disintegrate during the gradual disappearance of the yolk, as is the case with corresponding (yolk) cells in the Insecta.

2. Development of the External Form of the Body.

The development of the external form of the body has been repeatedly investigated more or less thoroughly in the cases of *Agalena*, *Clubiona*, *Epeira*, *Theridium*, *Lycosa*, and *Pholcus*, and has been found to follow a very uniform course. In spite of this fact, and although a large number of zoologists, among whom we may mention HEROLD, CLAPARÈDE, SALENSKY, BALFOUR, SCHIMKEWITSCH, LOCY, and KISHINOUYE, have investigated the subject, some points, especially in the earlier ontogenetic stages, still remain obscure. The chief difficulty is connected with the early rudiment of the embryo and the first appearance of segmentation.

At a time when the blastoderm is either approaching completion or is fully developed, there appears (probably on the later ventral side) the prominence known to us as the primitive cumulus, the significance of which has already been discussed (p. 41, etc.) From this there extends forwards a band which is distinguished by its white colour from the rest of the egg, and is caused by a marked thickening of the blastoderm (Fig. 23 *A*, CLAPARÈDE, BALFOUR). HEROLD mentions a comet-like structure which arises at an early stage on the surface of the Araneid egg, this comparison being apparently suggested by the band just described, together with the primitive cumulus (Fig. 23). The band soon widens at the end furthest from the primitive cumulus, and it becomes still broader as the thickening of the blastoderm extends out laterally from this region.

Such a lateral extension of the blastodermic thickening, starting from the band, implies that we regard the band itself, as well as the primitive cumulus, as thickenings of the blastoderm, which have arisen by active increase of cells at these points. According to **Salensky**, a depression appears in front of the primitive cumulus; this soon closes again, and is regarded by him as the blastopore. We are disposed to attribute the same significance to that thickening of the blastoderm which was mentioned above in the description of the formation of the germ-layers. We thus assume that the primitive cumulus lies at the future posterior end, and that the band runs out from it anteriorly. Its position therefore indicates the ventral surface. The latter is clearly recognisable as such at a somewhat later stage, the blastodermic thickening extending further, and finally becoming evident on the surface of the egg as a region shaped somewhat like an isosceles triangle (Fig. 23 *C*). The basal part of this triangle seems to appear first (Fig. 23 *B*), and then by degrees the parts nearer the apex. The base of the triangle corresponds to the rudiment of the cephalic lobes, the point to the posterior end of the embryo. According to this account, the primitive cumulus would occupy the apex of the triangle, and must be looked for in the posterior region (Fig. 23 *B*), and the band which developed at first and proceeded from the primitive cumulus (Fig. 23 *A*) would

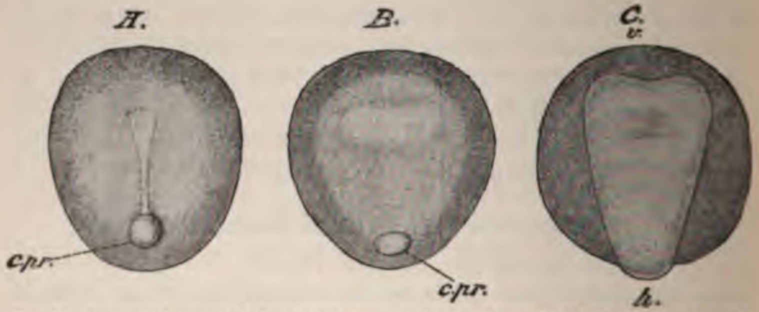

Fig. 23.—Superficial aspect of three early stages in the development of an Araneid, showing the embryonic rudiment (*A* and *B*, *Agalena labyrinthica*, after **Balfour**; *C. Theridium*, after **Morin**). *c.pr*, primitive cumulus; *h*, posterior; *v*, anterior.

then indicate the longitudinal axis of the embryo. The whole of the triangle thus represents the germ-band or the so-called ventral plate.

Embryonic envelopes, such as are found in the Scorpiones (p. 4), are wanting in the Araneae. The amniotic fold described by BRUCE on the head of the Araneid embryo must without doubt be referred to the infolding which takes place during the formation of the brain. The formation of cuticular larval integuments will be again referred to later (p. 58).

At about the time when the rudiment of the germ-band (the so-called ventral plate) first appears (Fig. 23 *A–C*), the egg is said to be flattened on this side, but at a slightly later stage the ventral surface of the embryo appears much arched (Figs. 24 and 25 *A*), either because this surface has become secondarily convex, or because this special region has not been affected. In *Pholcus* it appears to be the dorsal part that is flattened (Fig. 25 *A* and *B*), and CLAPARÈDE mentions that in this way the anterior and posterior ends are approximated.

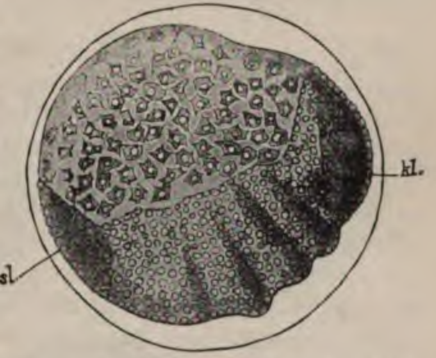

FIG. 24.—Young embryo of *Clubiona incompta* showing the commencement of segmentation of the germ-band (after SALENSKY). *kl*, cephalic lobe; *sl*, caudal lobe; between these are a few segments in the act of forming. The larger cells outside the region of the germ-band are said to represent blastoderm-cells which are here less crowded (SALENSKY).

The segmentation of the germ-band begins with the appearance of a few transverse furrows which mark off a large anterior and a posterior region, as well as several intermediate segments (Fig. 24). These segments at first appear very indistinct, the parts of the body to which they correspond being doubtful. In the youngest segmented stage, three segments were found besides the large anterior and posterior regions (Fig. 24, SALENSKY, BALFOUR, LOCY, LENDL). These seem to correspond to the first three thoracic segments.

According to LOCY, we must, however, assume that the three middle segments represent the second, third, and fourth thoracic segments. He believes that the segments develop in the following order; fourth, third, second, first thoracic segments, then that bearing the pedipalps, and last of all that carrying the chelicerae. The differentiation of the segments would thus take place from behind forward, an exact reversal of the order usually met with in segmented animals. There is a general resemblance between this view and that adopted by METSCHNIKOFF for the Scorpiones, according to which the embryos at first break up into three regions, the anterior corresponding to the cephalic region, the posterior to the telson, with the as yet undifferentiated segments of the post-abdomen, and the middle part giving rise to the other segments of the body (p. 6).

It is well to bear in mind how extremely difficult it is to orient the regions of the body in these early stages of the Araneid embryo (*cf.* Figs. 23–25). This difficulty throws some doubt upon the correctness of the identification of the body-segments, given above on SALENSKY's authority, and consequently the whole order of formation of the thoracic somites may be at fault.

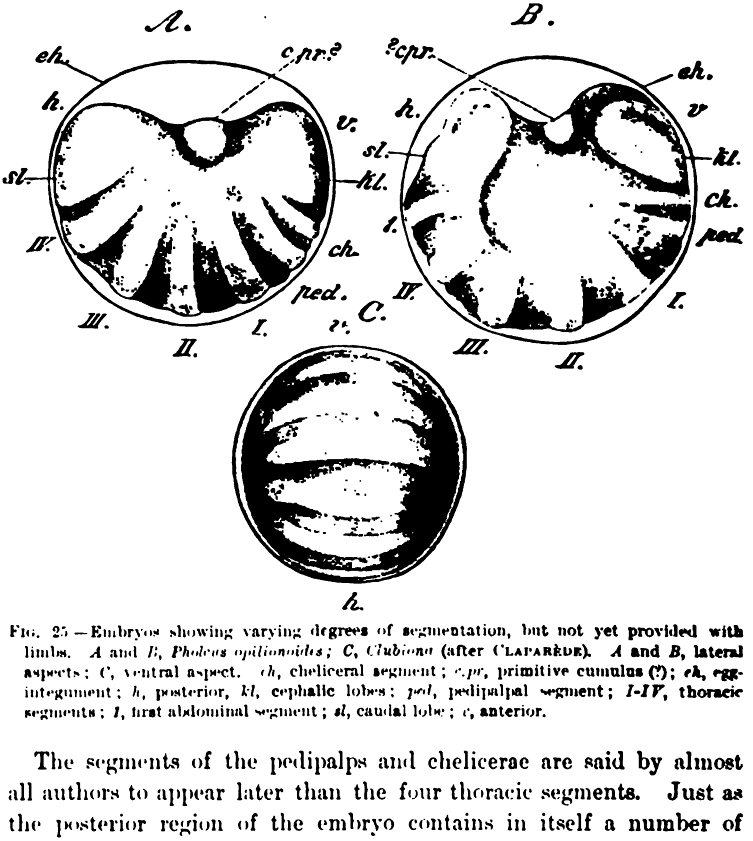

FIG. 25.—Embryos showing varying degrees of segmentation, but not yet provided with limbs. *A* and *B*, *Pholcus opilionoides*; *C*, *Clubiona* (after CLAPARÈDE). *A* and *B*, lateral aspects; *C*, ventral aspect. *ch*, cheliceral segment; *c.pr*, primitive cumulus (?); *eh*, egg-integument; *h*, posterior, *kl*, cephalic lobes; *ped*, pedipalpal segment; *I-IV*, thoracic segments; *1*, first abdominal segment; *sl*, caudal lobe; *v*, anterior.

The segments of the pedipalps and chelicerae are said by almost all authors to appear later than the four thoracic segments. Just as the posterior region of the embryo contains in itself a number of segments, so also does the anterior lobe comprise, besides the cephalic part, the segments of the chelicerae and the pedipalps. A regular separation of segments from before backward, therefore, does not take place. At the stage in which there are six segments interposed between the cephalic and caudal lobes (Fig. 25 *A* and *B*) the four posterior segments are much better developed and more distinctly marked off than the two anterior segments. BALFOUR, SCHIMKE-

WITSCH, and LOCY give figures of this stage in *Agalena*, in which the cheliceral segment is still united to the cephalic lobe, or is in the act of separating from it. We are unfortunately not able, from this description, to decide the order in which the thoracic segments become differentiated, but it seems as if the most posterior segment (the fourth) arose after the others. The abdominal segments separate from the caudal lobe in the usual order, *i.e.*, from before backward.

As the germ-band segments, it extends further over the egg; and not only do its anterior and posterior ends grow towards the dorsal side, but it extends laterally, and may thus, in a few forms (*e.g. Pholcus*), cover the greater part of the surface of the egg (Fig. 25 *A*). Seen from the ventral surface, the germ-band now appears broken up into segments, which extend transversely across the whole surface of the egg (Fig. 25 *C*). The segments appear somewhat narrow and as if separated by broad transverse furrows. The egg therefore somewhat resembles the dorsal surface of a rolled-up Isopod. This condition, however, is not long retained, a lateral contraction of the germ-band taking place which causes it to draw back again on to the ventral surface (Fig. 25 *B*), and to lie there in the form of a segmented band. The cephalic and caudal lobes retain their positions unchanged during this process, and, owing to the dorsal extension of the anterior and posterior extremities of the germ-band, they appear closely approximated (Fig. 25 *B*). In those forms in which the germ-band does not extend so far over the egg in early stages (*e.g. Agalena*), the cephalic and caudal ends only approach one another on the dorsal surface at a later period.

The shape of the germ-band becomes modified, the cephalic portion widening and assuming a bilateral, bilobed form; the abdominal segments, further, become separated from the caudal lobe, which has also widened. There may be as many as twelve abdominal segments besides the telson (*e.g.*, *Pholcus*, SCHIMKEWITSCH). *The abdomen is thus richly segmented in the Araneid embryo*, in direct opposition to its condition in the adult. The complete segmentation of the abdomen does not take place till the later stages, other important modifications in the germ-band preceding it. The first of these to be noted is the appearance of a longitudinal furrow in the ventral middle line (Fig. 28 *A*), which is caused by the division of the mesoderm lying on the ventral surface into two bands, these subsequently shifting to a more lateral position. The germ-band is in this way divided into two symmetrical halves (Figs. 28 *A* and

B, and 26), which may lie so far apart that the yolk protrudes between them (*e.g.*, *Agalena*, **Balfour**, Fig. 29, p. 53). Anteriorly, in the cephalic lobes and also at the caudal end, the two halves of the germ-bands remain united (Figs. 28 *A* and *B*, 26).

Long before the germ-band has divided to such an extent, the rudiments of the limbs have appeared, the first to be seen being those of the four pairs of ambulatory limbs, as slight prominences a little removed from the median groove (Fig. 28 *A*, *3–6*). These are followed by the rudiments of the pedipalps (*2*), and, a little later by those of the chelicerae (*1*). The rudiments of limbs arise in the same way on the first four abdominal segments (Figs. 28 *A*, *a*, 27), so that the *abdomen of the embryo is not only much more fully segmented than that of the adult, but even has limbs on some of its segments.* In this respect the Araneae resemble the Scorpiones, which also have limbs on the anterior abdominal segments (p. 8). Further similarity is found in the fact that, in the former, the posterior part of the abdomen may be flexed forward ventrally like the post-abdomen of the Scorpion embryo. This is the case in *Pholcus*, as was pointed out by **Claparède**, and confirmed by **Emerton**, **Schimkewitsch**, and **Morin**.

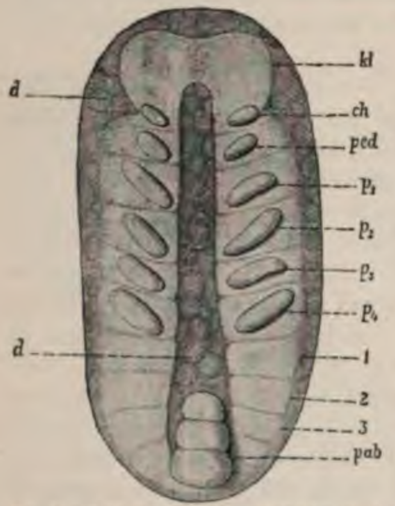

Fig. 26.—Embryo of *Pholcus opilionoides*, ideally unrolled (after **Claparède**). *ch*, chelicerae; *d*, yolk; *kl*, cephalic lobes; *ped*, pedipalps; p_1–p_4, first four pairs of limbs; *1–3*, first three abdominal segments; *pab*, the posterior part of the abdomen flexed ventrally.

It is almost universally admitted that the first four abdominal segments carry provisional appendages (**Balfour**, **Locy**, etc.). Even **Morin**'s researches, carried out by the help of the latest methods, yielded the same result, although **Salensky** had mentioned a first limbless segment, and **Schimkewitsch** had accepted this view. The statements of these two authors are supported by the notes and figures of **Bruce**, published after his death (No. 54). We were able easily to convince ourselves, by examination of an Araneid embryo (sp?), of the presence of a first abdominal segment (Fig. 27, *1*), which is quite as distinct as the following segments, and shows indications of a pair of abdominal limbs.* In *Agalena* also, which has been repeatedly examined, this segment is found, and the embryo, at a stage nearly corresponding to that illustrated in Fig. 27, shows indications of the rudiments of a pair of limbs. These rudiments are but slightly developed in *Agalena* (less so than in Fig. 27), and soon completely disappear. A similar condition of this first abdominal segment is found in other Araneids (KORSCHELT).

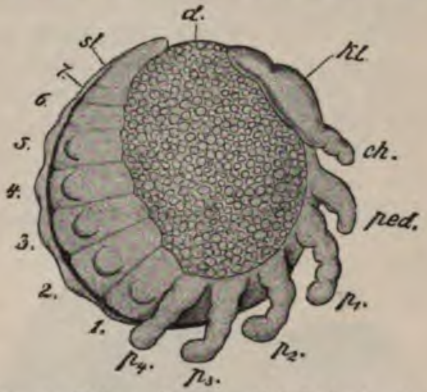

FIG. 27.—Embryo of an *Araneid* (*sp?*) showing the dorsal curvature of the germ-band and the rudiments of the abdominal limbs (original). *ch*, chelicerae; *d*, yolk; *kl*, cephalic lobe; *ped*, pedipalps; p_1–p_4, ambulatory limbs; *1–7*, abdominal segments, the provisional limbs being visible on the first five; *sl*, caudal lobe.

The first abdominal appendage is followed by others, varying in number from two to five, but usually by four, similar to those already described, and, finally, a much less distinct appendage seemed to be recognisable on the sixth segment in the form illustrated in Fig. 27. We should not have laid any stress upon this, as the sixth appendage was not sufficiently distinct, had it not been evident from CLAPARÈDE'S and EMERTON'S figures that in other Araneids (*Clubiona* and *Pholcus*) the sixth provisional pair of limbs is quite distinct. The appearance of six pairs of abdominal limbs is of importance in establishing great similarity between the Araneae and the Scorpiones. This similarity is specially seen in the further fate of the provisional limbs (p. 57).

The first abdominal segment seems, in many species, to undergo degeneration early. Nothing can be seen of it either in BALFOUR'S figures of *Agalena* (Fig. 28 *A* and *B*) or in the figures of LOCY, who examined another species of the same genus. In other figures by the latter author, however, the presence of this segment in the same species can be gathered with some certainty (Fig. 30 *A*). By other authors, the first segment which is provided with limbs, *i.e.*, the true second segment, has been considered as the first.

* Two recent investigators of the ontogeny of the Araneae, JAWOROWSKI (No. 5) and KISHINOUYE (No. 62), also state that in front of the segment which carries the first large pair of abdominal limbs, and which was usually taken for the first, another segment lies. These authors, however, did not find limbs on this segment. That such limbs may be present is shown by the above description and figure. [*Cf.* BRAUER on Scorpiones, No. II.]

The next modifications which take place can best be seen in the unrolled germ-band of an *Agalena* (Fig. 28 *A*). The most striking of these is the appearance of segmentation in the cephalo-thoracic limbs. From the basal joint of the pedipalp, a longitudinal furrow cuts off an anterior portion, which forms the masticatory blade, while the remaining much longer and jointed portion represents the palp (SCHIMKEWITSCH). The chelicerae remain for the time little modified, but they also soon become jointed. In front of them a new structure has appeared, the stomodaeum (*st*). Between the cephalic lobes, and towards their posterior edge, a depression appears; this at first is a pit, later a sac opening outwardly (Fig. 33, *m* and *vd*), and represents the stomodaeum. Near the mouth two paired structures appear (SCHIMKEWITSCH); two small prominences, which lie anteriorly near the oral aperture, and no doubt correspond to CRONEBERG's antennae (p. 111), unite immediately in front of the mouth to form the unpaired lip or rostrum. Two similar prominences are said to lie posteriorly to the oral aperture, and, fusing together, to yield a kind of lower lip. These two, the powerful upper lip and the slighter lower lip, the first forming an anterior and the second a posterior semicircle, enclose between them the oral aperture

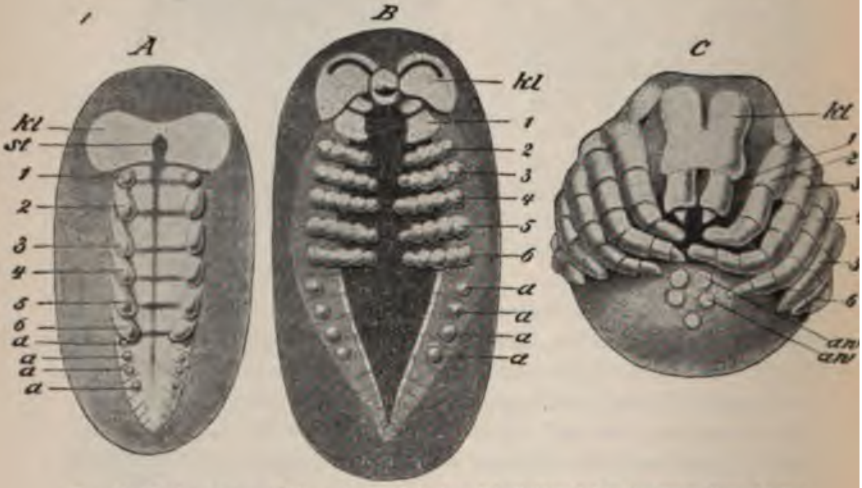

FIG. 28.—Various stages of the embryo of *Agalena labyrinthica* (after BALFOUR, from LANG's *Text-book*). *A* and *B*, ideally unrolled. Between 6 and *a* the fairly wide true first abdominal segment must be inserted. *a*, abdominal appendages; *an*, spinning mammillae; *kl*, cephalic lobe (in *B*, with the semicircular groove; between the two halves of the cephalic lobe is the mouth, surrounded by the upper and the lower lips); *st*, stomodaeum; *1*, chelicerae; *2*, pedipalps; *3*–*6*, limbs.

(Fig. 28). The characteristics of this stage are completed by the appearance of a semicircular furrow on each of the cephalic lobes (Fig. 28 *B*); this, as in the Scorpiones, is connected with the formation of the brain and of the eyes.

Up to this time the embryo shows a marked dorsal curvature, the continuous elongation of the germ-band causing the latter to assume the form of a nearly complete equatorial ring round the egg, and its cephalic and caudal extremities almost to touch one another (Fig. 27). On the dorsal surface at this stage, therefore, only a small part of the yolk is uncovered by the germ-band; this represents the future dorsal surface of the Spider, which is now about to commence to develop. This, however, alters in the stages that now follow, and that are characterised by the flexure of the embryo gradually changing from a dorsal to a ventral one.

The striking *reversal of flexure* or *reversion* of the embryo is due to a combination of the following changes: the growth of the dorsal surface (Balfour), the shortening of the germ-bands (Locy), and the transverse widening of the ventral groove between the two germ-bands.

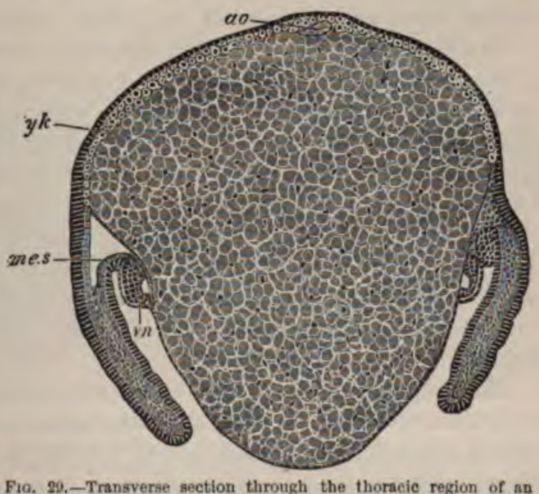

Fig. 29.—Transverse section through the thoracic region of an embryo of *Agalena labyrinthica* in the same stage as in Fig. 31 *A* (after Balfour). The section is made through that region where the ventral yolk-sac protrudes most. *ao*, aorta; *me.s*, mesoderm (primitive segment), which extends on each side up to the dorsal middle line; *vn*, ventral cord; *yk*, yolk with yolk-cells.

Until now the dorsal surface has remained practically undeveloped, the cephalic and caudal extremities of the germ-bands being situated in close proximity to one another on the dorsal surface. The limited cell-area between them now commences to grow, extending anteriorly and posteriorly, thus forcing apart these two lobes. At the same time a shortening of the germ-bands takes place (Locy), accompanied by a widening (due to growth) of the median ventral groove. This latter now becomes converted into a swelling, owing to the yolk pushing out the thin layer of cells, which unites the germ-bands ventrally, and forming a protrusion, the ventral yolk-sac (Barrois, Balfour), which soon completely separates the two halves of the germ-band from one another, causing the limb-rudiments, which formerly overlapped ventrally, to become widely separated (Figs. 29 and 31 *A*) and to move apart.

The middle portions of the two halves of the germ-band now gradually move dorsally, a change brought about more by the shifting of the yolk than by any growth of their own. And at the same time the two extremities of this band are pushed still further down until they reach the ventral surface.

As a direct consequence of these changes, *the previous dorsal flexure of the germ-band gradually undergoes a complete reversal of its curvature, and the germ-band finally assumes* a well-marked *ventral flexure*. These changes constitute the "reversion" of the embryo.

During these processes the growth of the dorsal surface proceeds only in a line with the long axis of the body, while it becomes narrower by the displacement of the two halves of the germ-band (*cf.* Figs. 27 and 30). The opposite condition obtains for the ventral surface, which we find shortening and widening, and finally converted into the temporary yolk-sac, which completely separates the two halves of the germ-band.

The completion of the reversal of flexure is reached when the abdomen is bent forwards ventrally (Fig. 28 *C*), *i.e.*, in a direction opposite to that which it formerly assumed. In *Agalena*, to which this description specially applies, a great reduction of the posterior abdominal segments is connected with this process (Fig. 31). These segments, when the change begins, rise somewhat from the yolk, so that the tail of the embryo resembles a loose flap lying on the yolk (Locy). The flexure-reversal of the posterior region of the body may thus be facilitated, and such a loosening helps us to understand the condition of *Epeira*. In this form the post-abdomen only degenerates at a later stage. Barrois describes a stage in the development of this Araneid in which the ventrally-curved embryo lying on the yolk-sac has, besides the four limb-bearing abdominal segments, at least six (perhaps even eight) others. The early development of the dorsal side of the abdomen, which has here taken place, is more easily understood on account of its loose attachment to the yolk. The change in the position of the yolk from the dorsal to the ventral side is specially marked in *Epeira*. The embryo itself, with its long abdomen, the anterior segments of which are broad, while the posterior are narrow, bears, if we may trust BARROIS' account, a decided resemblance to the Scorpiones.

BARROIS gives such distinct figures of this stage, both in dorsal aspect and in profile, that we should not hesitate to accept his description were it not denied by other authors that the dorsal segmentation described by him is actually present (SCHIMKEWITSCH, Nos. 12, *b*, and 72).

The rich segmentation of the abdomen, ten or even twelve segments being sometimes found, gives the embryo, before flexure-reversal (or perhaps sometimes, as in *Epeira*, shortly after that process) an appearance quite unlike that of an Araneid. A change, however, is brought about through the great development of the anterior abdominal segments, especially of those which carry the rudiments of limbs, this being accompanied by the reduction of the other segments. This process can be observed in *Agalena* at an early stage of flexure-reversal. According to LOCY, the anterior abdominal segments grow with unusual rapidity towards the dorsal side. Fig. 30 *A*, which illustrates the stage under consideration, represents the postero-lateral aspect of the embryo, so that the anterior abdominal segments can be recognised at each side growing up dorsally. Between them lies the bent caudal lobe (*sl*), and the yolk-sac (*d*) already appears on the ventral side in this region. The

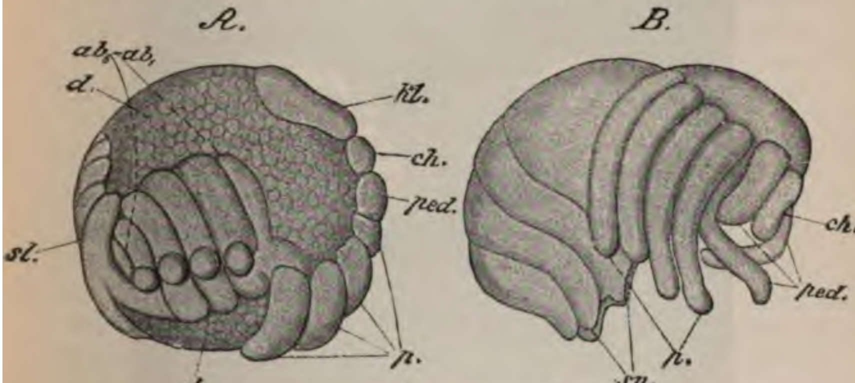

FIG. 30.—Older embryos of *Agalena naevia*, *A*, showing the commencement of the flexure-reversal. *B*, having completed the flexure-reversal, and near hatching (after LOCY). The embryo in *A* is viewed somewhat obliquely. ab_1–ab_6 the first abdominal segments, four of which carry the provisional limbs; *d*, yolk; *ch*, chelicerae; *ped*, pedipalps; *p*, the four ambulatory limbs of the right side; *kl*, cephalic lobe; *sl*, caudal lobe; *sp*, spinning mammillae (provisional abdominal limbs).

larger abdominal limb-rudiments are still distinctly visible $(a_2–ab_5)$. This figure further shows very distinctly the presence (already alluded to) of an abdominal segment lying in front of that bearing the first provisional limb (ab_1). This segment, as well as the one which follows the last limb-bearing segment, also takes part in the growth towards the dorsal side. From this figure and others taken from Locy, we gather that the segmentation of the dorsal side is, in this part of the body, a true segmentation, and that the segmentation observed by Barrois on the dorsal side of an Epeirid embryo is to be regarded in the same way. It seems advisable to point this out, because the embryo of *Epeira* has such a characteristic form even in later stages. The external segmentation is the expression of the dorsal extension of the primitive segments, which arise in the Araneae as in the Scorpiones, by the segmentation of the mesoderm-band (pp. 23 and 85).

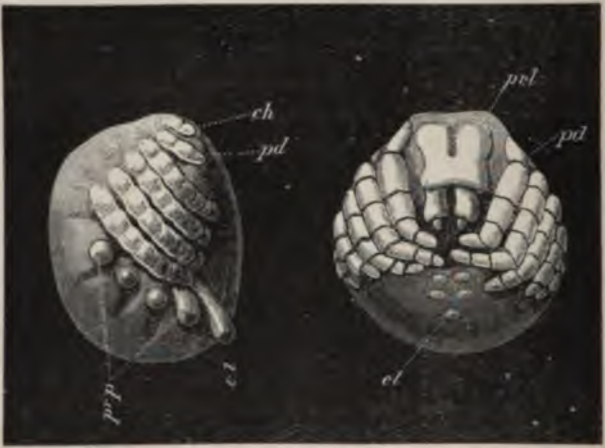

Fig. 31.—Two older embryos of *Agalena labyrinthica* (after Balfour). *A*, embryo seen from the side with the large ventral yolk-prominence. The angle formed by two lines, one drawn through the points of origin of the thoracic limbs, and the other through those of the abdominal limbs, indicates the degree of ventral curvature. *B*, embryo shortly before hatching. The abdomen, which has not yet fully attained its permanent form, is pressed against the ventral side of the thorax. *ch*, chelicerae; *cl*, caudal lobe; *pd*, pedipalps; *pr.l*, cephalic lobes; *pr.p*, provisional abdominal appendages.

The further development of the external form of the body, apart from the reduction of the caudal region just described, is determined by the union in the middle line of the halves of the segments that lie on each side. During this process, the principal mass of the yolk is withdrawn into the abdomen, and the cephalo-thorax and abdomen now become marked off from one another (Fig. 30 *B*). The dorsal part of the former is not extensive, and shows no traces of segmentation.

The cephalic region has undergone considerable modification, the cephalic lobes being smaller than before (Figs. 30 and 31). The chelicerae are no longer post-oral, but have attained a pre-oral position (Fig. 31 *B*). Between them the upper lip or rostrum has formed.

The half segments, which became united dorsally, now join on the ventral surface, after the ventral nerve-strand, which arose by the thickening of the inner edge of the two halves of the germ-band, has become detached and has been drawn inward. As has already been mentioned, it is the anterior abdominal segments which, by their active growth, give rise to the large spherical abdomen of the Araneid. We might compare them to the pre-abdomen of the Scorpion. The posterior segments, which are comparable to the post-abdomen of the latter, however, degenerate either totally or to a great extent. The long abdomen of the embryo gives place to the compact abdomen known to us in the adult.

An important point hitherto left unnoticed is the fate of the abdominal appendages. These, as rudiments, resemble the thoracic limbs, as can be seen from Fig 31 *A*; while, however, the latter grow and become jointed, the former decrease in size and become button-like. During the flexure-reversal, and even after it, they retain the same shape and position (Figs. 30 and 31 *A*). Then, however, they begin to change. At the base of the limbs of the second segment, the ectoderm becomes invaginated to form the lung-sacs, [and respiratory organs are similarly developed on the third segment. The fate of the first abdominal segment is still uncertain. This segment, so long overlooked (*cf.* p. 51, Fig. 27, *1*, and footnote), is now recognised by BRAUER and PURCELL as the homologue of that small and almost limbless first abdominal segment which BRAUER discovered in the Scorpiones, and of the disputed segment bearing the metastoma in *Limulus* (KISHINOUYE and PACKARD, Vol. ii., p. 345, footnote). If this comparison is correct, *the genital segment in all the three groups is proved to be the eighth post-oral segment* (*i.e. the second abdominal segment in the Scorpiones and the Araneae*).] The third segment (BRAUER) of the Scorpiones yields the combs, which are structures peculiar to this group. The fact that the segment which, in the Scorpiones, carries the combs, may develop lungs in the Araneae is explained by reference to Limulus, in which it carries gills.*

The appendages of the third segment (see above) are said to

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* [BRAUER, App. to Lit. on Scorpiones, No. II., PURCELL, App. to Lit. on Araneae, No. VII.]

degenerate, while those of the fourth and fifth segments become changed into spinning mammillae (Figs. 30 and 31, SALENSKY, LOCY, MORIN). On these mammillae the spinning glands arise as ectodermal invaginations (Fig. 46, *spw*, p. 88). If the spinning mammillae are reduced limbs (p. 79), we must regard the glands as belonging to the order of crural glands, having a phylogenetic origin similar to that of the corresponding structures in *Peripatus*, the Myriopoda and the Insecta. The anus arises on the last abdominal segment at the completion of flexure-reversal, when the post-abdomen is already degenerating, as an ectodermal invagination.

When the young Araneid leaves the egg-integument it is, in many cases, quite incapable of movement. It continues for some time (in many forms for some days) in the same place without any movement being apparent in it. It is invested more or less closely by a structureless envelope, the first embryonic cuticle, beneath which the future hairy covering is already present. This outer cuticular envelope, which may to some extent be regarded as a larval integument, is broken through after a time, but the young Araneid is still somewhat helpless; it can, indeed, move its limbs, but it can only move from place to place freely after several moults. The young of *Epeira cornuta*, on the contrary, is able to move to a considerable extent when it leaves the egg (PURCELL).

It is an interesting fact that the first cuticular integument may be provided with a kind of *egg-tooth*, which serves for splitting the egg-shell. According to the researches of F. PURCELL, there is, at the base of the two pedipalps of *Tegenaria domestica*, a thickened plate-like part of the first chitinous integument, which, in contrast to the rest of the cuticular covering, appears dark in colour—almost black. From this spot an outwardly projecting spine arises, such as was described above as an egg-tooth. A similar but less developed spine is found in a corresponding position in *Attus floricola*, and also in a *Xysticus*. It may also occur in other Araneids. PURCELL observed that the first rent takes place in the chorion, immediately over the egg-tooth. It extends from this point, and soon a cap-like portion of the egg-integument is separated off. The movements of the embryo, which must take place to produce the splitting of the egg-shell, could not be noticed. The spine, having fulfilled its function in splitting the egg-integument, is thrown off with the cuticular envelope. We shall find a similar arrangement in the Myriopoda, in which also an egg-tooth belonging to the cuticular envelope develops. The same is the case in the Opiliones (p. 33).

3. The Development of the Organs.

A. The Nervous System.

The ventral chain of ganglia arises shortly after the appearance of the limbs, as ectodermal thickenings on the inner side of their bases (Fig. 32 *A*). Even before the formation of the limbs, a thickened longitudinal band of ectoderm appeared on each side near the middle line, the two bands being separated by a thin median ectodermal strand. This thickening first appears in front, and grows backwards. A pair of such swellings (ganglia) belongs to each segment. (BALFOUR, LOCY). In the cephalo-thorax there is a pair each for the segments of the chelicerae and the pedipalps, as well as for the four pairs of ambulatory limbs. In the abdomen as many as ten pairs of ganglia (in *Pholcus*, according to SCHIMKEWITSCH, twelve) may appear. The longitudinal commissures connecting the ganglia are represented by thinner portions of ectoderm; but the transverse connectives are not yet developed, the ganglia being still separated by a thin layer of ectoderm (Fig. 32 *A*). This is still more striking later, when the two halves of the germ-band shift apart (Fig. 32 *B*, *n*). The two strands of the ventral chain of ganglia, which at first lay near the middle line, are widest apart when the yolk is pressed towards the ventral side, so as to form the so-called yolk-sac (Figs. 32 *B* and 29,

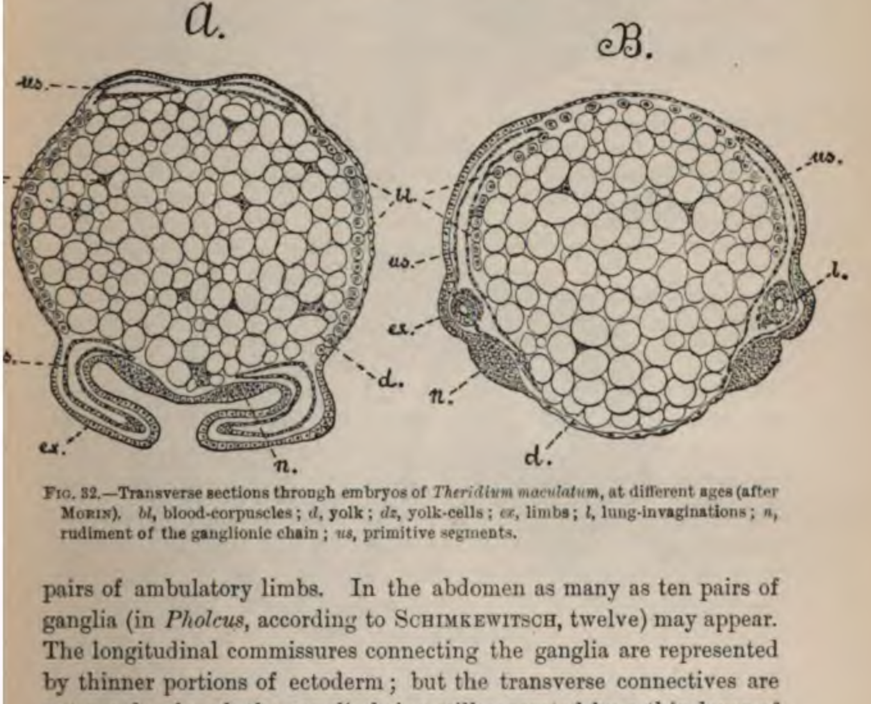

FIG. 32.—Transverse sections through embryos of *Theridium maculatum*, at different ages (after MORIN). *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk-cells; *ex*, limbs; *l*, lung-invaginations; *n*, rudiment of the ganglionic chain; *us*, primitive segments.

p. 53). Before this happens, however, various modifications have taken place in the length of the chain; the ganglia also gradually lose their connection with the ectoderm, and come to lie internal to it (Fig. 48 *B* and *C*, p. 92).

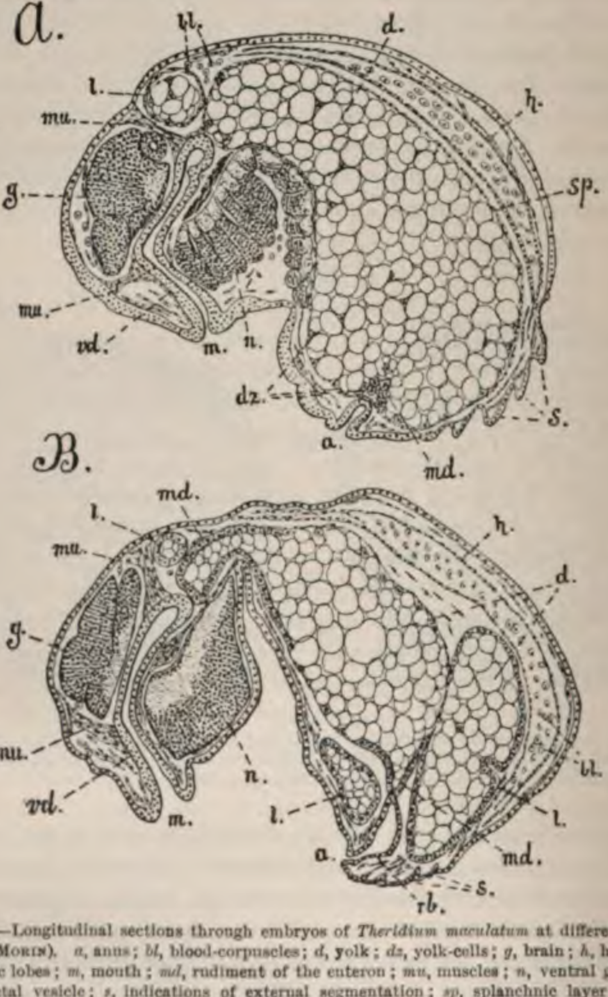

FIG. 33.—Longitudinal sections through embryos of *Theridium maculatum* at different ages (after MORIN). *a*, anus; *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk-cells; *g*, brain; *h*, heart; *l*, hepatic lobes; *m*, mouth; *md*, rudiment of the enteron; *mu*, muscles; *n*, ventral ganglia; *rb*, rectal vesicle; *s*, indications of external segmentation; *sp*, splanchnic layer of the mesoderm; *vd*, stomodaeum.

When the germ-band still shows a dorsal curvature, the ventral chain of ganglia also extends round the whole of the yolk, but, as the germ-band reverses its flexure, it shortens, the concentration taking place from behind forward (LOCY). Thus while that part of the chain lying in the cephalo-thorax increases greatly in size, that in the abdomen shortens (Fig. 33 *A* and *B*). The separate ganglia have already come together to form two thick strands. At first the large ganglionic mass in the cephalo-thorax is still connected with a strand of abdominal ganglia (Fig. 33 *A*), but, as the growth of the embryo progresses, the latter also is drawn into the common ganglionic mass in the cephalo-thorax, at least this appears to be the way in which we must interpret the process. At first the individual ganglia, though closely pressed together, are still externally distinct (Fig. 33 *A*), but they become less distinguishable later (LOCY, MORIN).

By the approximation of the two halves of the germ-band, which occurs through the reduction of the yolk-sac, the two portions of the ganglionic chain again approach each other, and transverse commissures now form.

BALFOUR, in describing the formation of the transverse commissures, speaks of the appearance of delicate connecting fibres in the dorsal region of the ganglia, and expressly denies that a median ectodermal invagination takes part in the formation of the ganglionic chain. SCHIMKEWITSCH, on the contrary, expresses himself quite as decidedly in favour of the presence of such a median strand appearing like a shallow groove between the two approximated ventral nerve-trunks (Fig 48 *B* and *C*, p. 92).

It has already been pointed out (p. 12) that an unpaired median strand participates in the formation of the ganglionic chain in the Scorpiones, and we must assume that this, in both cases, gives rise to the transverse commissures.

As the concentration of the ganglionic chain commences, the formation of nerve-fibres becomes evident, appearing first in the dorsal part of the ganglia, *i.e.*, at the part where, according to BALFOUR, the transverse commissures arise (Fig. 33 *A* and *B*). When the chain has become highly concentrated, the separate pairs of ganglia are still indicated by the transverse commissures. The elongate ganglionic chain of the earlier stages is now reduced to the comparatively short and bulky ganglionic mass in the cephalo-thorax, such as is found, though smaller, in the adult. Only one important modification has still to be mentioned. The pair of ganglia belonging to the cheliceral segment, which at first is post-oral, shifts later to a position in front of the mouth, fusing with the brain, and at the same time forming the anterior part of the oesophageal commissure. The posterior portion of the latter, *i.e.*, the part lying directly behind the oesophagus, is formed by the ganglia of the pedipalps.

As far as we can gather from the statements of BALFOUR, SCHIMKEWITSCH, LOCY, and MORIN, the fusion of the ganglia of the cheliceral segment with the brain seems to take place very early, and we may perhaps, therefore, assume that their transverse commissure is from the first formed in front of the oesophagus. This commissure has been described by BALFOUR.

The Araneae resemble the Scorpiones with regard to the fusion of the cheliceral ganglia with the brain, and we would here call attention to what is perhaps a corresponding process in the Crustacea and in *Peripatus* (fusion of the ganglia of the second antennae or maxillae with the brain, Vol. ii., pp. 163, 165, and Vol. iii., p. 193). According to SCHIMKEWITSCH, there is another pair of ganglia between the cheliceral ganglia and the brain, which corresponds to that part of the brain which gives origin to the (unpaired) rostral nerve. To this point we shall return later.

After the ganglia have assumed the above-mentioned position, they become closely surrounded by a thin layer of mesoderm, which further grows in between the cell-masses and between the fibrous strands. This gives origin to the neurilemma and the trabecular network between the separate parts of the ganglia (SCHIMKEWITSCH). This is also said to take place in the Crustacea (Vol. ii., p. 162).

The supra-oesophageal ganglion originates as a large thickening of the cephalic lobes. According to KISHINOUYE (No. 62) the rudiment of the brain is continuous with those of the ganglionic chain, these rudiments forming together two longitudinal bands running from before backward. There are at first two distinct thickenings of the cephalic lobes, one on each side, bounded anteriorly by the semi-lunar furrow already described (Fig. 28 *B*). These furrows become deep and narrow slits, which appear to be lined with an epithelium, and remain in close connection with the rudiment of the brain. When this latter becomes detached from the surface layer, the invaginated ectodermal parts also become cut off from this layer as closed vesicles, and form an integral part of the supra-oesophageal ganglion (SALENSKY, BALFOUR, MORIN). The invaginate lining of the semi-lunar depressions (cephalic pits) yields the upper hemispherical lobes of the brain; the cavities being retained for some time at the sides. Between the two central masses fibres form, giving rise to the commissures that connect the two halves of the brain. BALFOUR further distinguishes a ventral region lying immediately in front of the cheliceral ganglia, which perhaps corresponds to the rostral ganglia described by SCHIMKEWITSCH.

The manner in which the brain forms in the Araneae has not yet been ascertained with sufficient certainty; but various accounts given tend to confirm the view that the brain arises here, as in the Scorpiones, as a paired thickening of the ectoderm in connection with paired ectodermal invaginations. These invaginations of the cephalic lobes seem to show great resemblance in the two groups, but it is not ascertained that they share in the Araneae, as in the Scorpiones, in the formation of the eyes. On the contrary, it appears from the published statements that the optic rudiments arise quite independently of the semi-lunar depressions. We are inclined, nevertheless, to assume that the part of the brain arising from infolding perhaps corresponds to the optic ganglion, and that the folds which yield the eyes later enter into relation with it. The middle part of the brain (protocerebrum, ST. REMY, No. 12) might be traced back to the thickening of the cephalic lobes, while the posterior part—the rostro-mandibular ganglion—is probably to be regarded as a part of the original chain of ganglia, as has already been shown.

This conjecture as to a connection of the cephalic pits with the optic rudiments is confirmed in a recent work by KISHINOUYE (No. 62). This work differs from former publications on the subject of the development of the Araneid eye, in actually assuming a connection of the eyes (anterior median eyes or principal eyes) with the cephalic pits, and thus, in this respect, establishes greater agreement with the Scorpiones. KISHINOUYE further found three segments in the developing brain, such as PATTEN assumed for the rudiment of the brain of *Scorpio* (p. 18). Unfortunately, the statements of both these authors are not sufficiently clear to enable us to understand their detailed accounts of the development of the brain, and to bring them into agreement with the statements of earlier observers. KISHINOUYE's accounts do not in any way agree with PATTEN's, as may be seen by the relation of the optic rudiments to the different sections of the brain. The former describes an invagination which is independent of the cephalic pits; nothing certain is known, however, as to its relation to the segments of the brain. Interesting and important conclusions may be expected from thorough investigation of this subject.

The statements of SCHIMKEWITSCH, that the cavities in the rudiments of the brain are not to be derived from infoldings of the ectoderm, but owe their origin to a later process of folding of the ganglionic mass after separation from the ectoderm, contradicting the views of other authors, can meet with no approval.

B. The Eyes.

The eyes, in the Araneae, arise through a process of infolding which closely resembles that described in connection with the median eyes of *Scorpio*; special modifications, however, occur in the Araneae. Until lately a connection between the eye-folds and the depressions on the cephalic lobes was not assumed; it was thought, rather, that the optic pits first arose when the cephalic pits had already closed.* The formation of the former certainly occurs at a late period in the development of the embryo, commencing when the latter is nearly completed. There then appear, in the frontal region, several pairs of (transverse?) slit-like depressions lying near each other, or one behind another. In *Pholcus* there are said to be two (CLAPARÈDE), in *Lycosa* three pairs, but our knowledge as to these depressions and

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* [This view will be materially modified by the observations of KISHINOUYE, mentioned below, should they prove correct.—ED.]

their position is so slight that nothing definite can be asserted about them. It appears, however, to be certain that the four pairs of eyes arise from different infoldings (Mark).

The way in which the different eyes arise varies, the anterior median pair differing in this way from the two posterior median eyes, and from the two lateral pairs. There is a corresponding difference in structure: in the anterior median eyes the rods of the retinal cells lie external to the nuclei (Fig. 34 *A*, *st*), while in the other eyes the rods are found internal to the nuclei (Fig. 34 *B*, *st*). In the first case, the nuclei lie at the base of, in the second, at the outer ends of, the retinal cells. The anterior median eye, further, has no tapetum (Fig. 34 *B*, *t*), *i.e.*, no layer of cells lying behind the retina filled with shining granules, such as occurs in the other eyes, and apparently also determines a difference in their methods of development. Following Bertkau, we shall, for the sake of brevity, call the anterior median eyes *principal eyes*, the posterior and lateral eyes *accessory eyes*. These two kinds of eyes are distinguished, not only in structure, but possibly also in the method of their development (see below), a fact which justifies us in making this distinction. The last point, however, requires further elucidation.

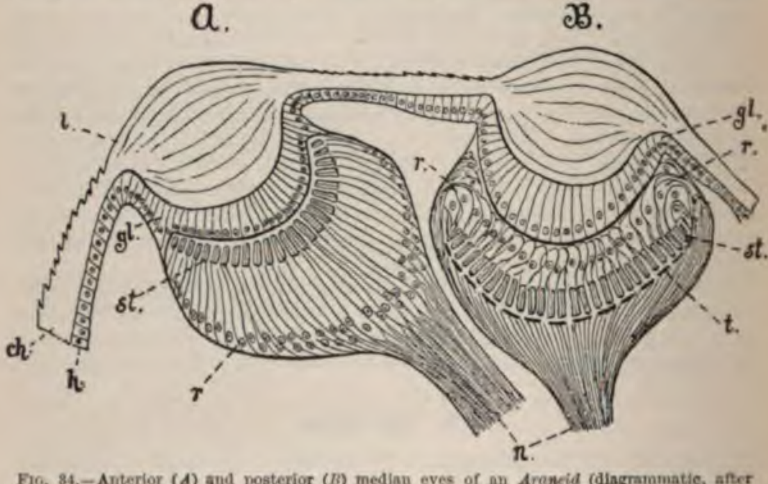

Fig. 34.—Anterior (*A*) and posterior (*B*) median eyes of an *Araneid* (diagrammatic, after Grenacher and Bertkau). *ch*, chitinous covering of the body; *gl*, vitreous body; *h*, hypodermis; *l*, lens; *n*, optic nerve; *r*, retinal cells; *st*, rods; *t*, tapetum.

Our present knowledge concerning the origin of the eyes in the Araneae is chiefly due to the researches of Locy (No. 64) and Mark (No. 67), carried out on *Agalena naevia*. The following account, therefore, refers specially to this form. Kishinouye (No. 62), recently made some investigations of the development of the Araneid eye in *Agalena* and *Lycosa*. His results differ in some essential points from those of his predecessors, and, if confirmed, are of importance for the comprehension of the Araneid eye.

The anterior median eyes (principal eyes) are first seen as ectodermal thickenings of the frontal region. In front of this thickening an invagination appears (Fig. 35 *A*, *a*), which eventually carries in the whole of the thickened area (Fig. 35 *B*). The deep sac thus formed is directed posteriorly, and becomes applied to the ectoderm, which now shows a second thickening (Fig. 35 *B*, *l*). In further explanation of this stage we refer the reader to Fig. 10 *B*, p. 14, which illustrates the very similar course of development of the median eye in the Scorpion. Here, as there, the ectodermal (or hypodermal) layer lying over the sac forms the vitreous body, and secretes the lens on its outer side (Fig. 35 *B* and *C*, *l*). The aperture of the invagination (*a*) closes, and the optic vesicle thus becomes cut off from the ectoderm. The cells of the already thickened (outer) wall of the invagination lengthen distally, their nuclei taking up a position furthest from the surface, as can be seen in Fig. 35 *C*. The rods are then secreted at the distal ends, and thus lie external to or in front

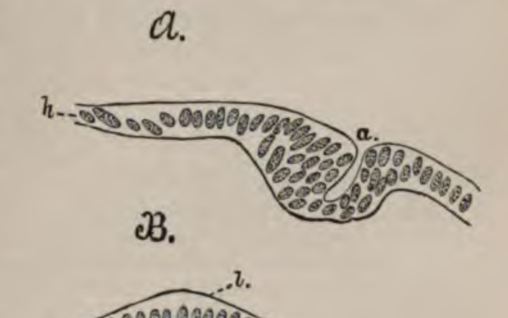

FIG. 35.—Development of the principal eyes of *Agalena naevia*, sagittal section (after LOCY). *a*, optic invagination; *gl*, vitreous body; *h*, hypodermis; *l*, lens; *pr*, post-retinal layer; *r*, retina.

of the nuclei. The whole of this thickened layer represents the retina, while the thin lower wall of the invagination (*pr*), the so-called post-retinal layer, perhaps yields the posterior enveloping layer of the eye (LOCY). A displacement of the nerve, in relation to the retinal elements, must take place here, as in the eye of *Scorpio*, since the former, in the adult eye, is connected with the posterior ends of the retinal cells (Fig. 10 *A* and *C*, p. 14, and Fig. 34 *A*).

The posterior median eyes and **the two pairs of lateral eyes (accessory eyes)** also arise through infoldings of the ectoderm, which are directed posteriorly, and become applied to the ectoderm (hypodermis). The lens is then secreted above the infolding (LOCY, MARK). Up to this point the formation of these eyes appears to agree with that of the anterior median eyes.

In the anterior lateral eyes the invagination is, according to MARK, directed anteriorly. Perhaps this fact accounts for the number of the optic folds as described by CLAPARÈDE, the anterior eyes arising separately, while the posterior eyes originate from a common fold. This is, indeed, merely a conjecture, which we are led to make by the difficulty of gaining, from the statements before us, any exact idea of this important process.

The development of the posterior median eyes and that of the lateral eyes further differ in that the formation of the rods occurs not in the outer, but in the inner parts of the retinal cells. The nuclei take up an external position, and the cells lengthen in the direction of the cavity of the optic vesicle, and secrete the rods on their inner ends. In consequence of this, the rods here lie behind the nuclei, a position similar to that found in the eye of the adult (Fig. 34 *B*).

While the outer wall of the invagination is transformed into the retina, as in the anterior median eyes, the inner part seems to undergo another process of folding (MARK). The new fold extends into the original cavity of the first invagination, and represents the rudiment of the *tapetum*. Its cells secrete later the small crystals which cause the glitter of the adult eye. The post-retinal layer behind the tapetum-fold here also bounds the eye posteriorly (MARK).

According to LOCY, the tapetum owes its origin to a continuation of the outer chitinous covering of the body into the primitive eye-fold. But since the tapetum is of a cellular nature, as was shown by BERTKAU'S researches (No. 52), this does not appear very probable. Another view concerning the origin of the tapetum, which has been repeatedly suggested, is that it consists of migratory mesoderm-cells laden with a silvery pigment.

A displacement of the nerves and of the retinal elements need perhaps not be assumed in these eyes, for, according to BERTKAU, the nerve in the Araneid eye always joins the optic cells at the ends at which the nuclei lie (Fig. 34 *A* and *B*). In the present case, this is the distal side of the retina; the nerve has therefore retained its original position.

It appears, from BERTKAU's account, that the nerves join the distal (external) ends of the optic cells (Fig. 34 *B*), the nerve-fibres running from the periphery to the ends of the cells. This seems to be the most primitive arrangement. BERTKAU, however, states that nerve-fibres also traverse the tapetum (Fig. 34 *B*) and run to the distal ends of the cells (*i.e.*, in between the optic cells). This latter course taken by the nerves must be regarded as secondary, if we consider the processes of development, for a perforation of the post-retinal layer then takes place.

It is possible to reconcile BERTKAU's description with the views founded by MARK upon ontogenetic researches. According to these, some of the nerve-fibres run round the tapetum to join the distal ends of the retinal cells; others, however, are said to traverse the post-retinal layer as well as the tapetum.

Additional remarks on the development of the principal and the accessory eyes. The statements of KISHINOUYE, as we have already remarked, would, if confirmed, be of importance in affecting our view of the development of the Araneid eye. According to this writer, the principal eyes arise through inversion, essentially in the manner described above. An important point is found in the fact that the aperture of invagination represents also the last trace of the aperture of the closing cephalic pit. The (anterior) median eyes are thus, as in the Scorpiones, related to the invaginated part of the cephalic lobes, a fact which could not be gathered from the descriptions of earlier authors.

While the principal eyes arise through inversion, the accessory eyes, according to KISHINOUYE, have quite another origin, being formed by a *mere depression of the ectoderm without inversion.* They appear later than the principal eyes, and lie behind these. It appears that they are related to the invaginations mentioned above, which form independently of the cephalic pits, and take part in the formation of the brain. This recalls the formation of the optic ganglia. The accessory eyes seem to arise independently of one another as pit-like ectodermal depressions. The base of each of the depressions thickens considerably, and becomes the retina. The nerve joins the retina posteriorly, so that there is no suggestion of inversion, and the whole resembles the eye of the Insecta. The pit closes, its lips growing together and fusing. These parts yield the vitreous body, above which the lens is secreted.

If the Araneid eyes actually form in the manner here described, they would show great agreement with the eyes of the Scorpiones. *The anterior median eyes of the Araneae, which develop through inversion, would then correspond to the median eyes of Scorpio, which arise in a similar manner; the posterior median and the lateral eyes of the Araneae would be comparable to the lateral eyes* of the Scorpiones, which also originate as *simple ectodermal depressions* (*without inversion*). If so, BERTKAU's division of Araneid eyes into "principal" and "accessory" eyes would have some significance.

The fact that these very important results obtained by KISHINOUYE were not accorded the first place in our account is partly due to their becoming known to us only during the publication of this book. Again, compared with the statements of former investigators, they did not appear sufficiently supported. It should be noticed, however, that researches made by F. PURCELL, independently of the work of KISHINOUYE, on the structure and development of Araneid eyes, led to similar results. PURCELL also thought that the lateral eyes arose in the form of slight depressions of the ectoderm, over the bases of which (retinae) the lateral parts grow in as vitreous bodies. This seems to agree with the structure of the adult eyes, which, together with PURCELL's ontogenetic observations, will be further examined later on.

C. Survey of the Arachnidan Eyes.

In order to understand the development and structure of the Araneid eyes, it is necessary to compare them with the eyes of the Scorpiones. Whereas the eyes of the Araneae are usually regarded as simple eyes, *i.e.*, as so-called ocelli, the retinae of which show no regular grouping of cells (retinula formation, Fig. 34 *A* and *B*); the eyes of the Scorpiones have retinulae, *i.e.*, groups of cells with a central rhabdom* (Fig. 11 *B*, p. 17, and Fig. 10 *C*, p. 14). The eyes of *Scorpio*, especially the median eyes, thus show an essential feature of the compound eye, although, like the Araneid eye, they possess a single corneal lens not divided into facets, and therefore are without another important feature of the compound eye. We must, nevertheless, regard them as compound eyes, if only as modified eyes of this sort, as will be proved by the following considerations.

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* In the simple Arthropodan eye (*ocellus*, *stemma*, etc.) the retina consists of a layer of similar optic cells (Fig. 36, *r*); in the compound eye, however, it breaks up into groups of cells, the *retinulae* (Fig. 10, p. 14). These cells, which vary in individual cases, carry, at the sides which are turned towards the centre of the group, optic rods (*rhabdomeres*), which may fuse to form a single structure, the *rhabdom* (Figs. 37, *rh*, and 10, p. 14). Each group of the retinulae, together with the superjacent cells of the vitreous body and the corneal facets belonging to them, forms one of the ommatidia (Fig. 198 *D*), which in larger or smaller numbers compose the eye. This at least applies to the typical form of compound eye; the Arachnidan eye now under consideration is somewhat different.

In tracing back the Arachnid eyes to compound eyes, in order to understand their structure, we must first explain the origin of the latter. It facilitates matters if we refer to the probably analogous conditions in the Insecta. The simplest eyes (ocelli) of the latter are pit-like depressions of the hypodermis, over each of which lies a single lens. Corresponding simple eyes are found in the Annelida; these are mere pits in the body-integument, richly pigmented and with a lens lying in each (*Diopatra* and *Onuphis*, v. KENNEL, No. 60). The ocelli of the Insecta are on a somewhat higher level, the hypodermal layer bulging inwards from the sides over the retina, and thus forming the so-called vitreous body beneath the lens (Fig. 36, *gk*). In the Myriopoda, the Insect larvae, and the Thysanura, a number of such ocelli are found grouped together. If we imagine their number still further increased, and a closer connection formed between them, we have the beginning of a compound facet-eye. In the Myriopoda, especially in *Scutigera*, such a condition seems actually attained. The eye which has thus arisen has at first no kind of uniformity. Its constituent parts seem still to be independent structures of too complicated a nature to permit of co-operation. A gradual reduction of the elements occurs in the single eyes, and, as it progresses, leads to the result known in the compound eye, viz., to the retention of only a few of the elements of each primarily single eye. The single eye has in this way become an ommatidium. We thus imagine the ommatidia as arising out of ocelli. The rationale of this process, which led simultaneously to the reduction of the elements in the ocellus, and to an increase in number of ocelli, must be sought in the function of the compound eye, which requires the utmost attainable diminution of the visual surface in the single eye.

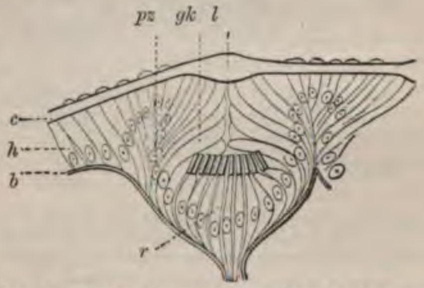

FIG. 36.—Section through the ocellus of a *Dytiscus* larva (after GRENACHER, from HATSCHEK'S *Text-book of Zoology*). *b*, basal membrane; *c*, chitinous cuticle; *gk*, vitreous body; *h*, hypodermis; *l*, lens; *pz*, pigment-cells; *r*, retina.

Such very simple eyes as the ocelli of the Insecta are not found in the Arachnida, but we must presuppose the presence of similar structures in their ancestors. The most simple Arachnidan eye is the *lateral eye of Scorpio* (Fig. 11 *B*, p. 17), a unilaminar eye, in the form of a pit, filled by the lens; the floor of this pit (the retina) being directly continuous with the hypodermis. Although this eye possesses, in the above features, the principal characters of a simple eye, we are not able to regard it as such, on the one hand, because of its detailed structure, and, on the other, because of the striking agreement existing between the eye of *Scorpio* and that of *Limulus*. The lateral eyes of the latter are unilaminar, as are those of *Scorpio*, while the median eyes in both forms consist of two or three layers. The lateral eyes of the Scorpiones, as well as those of *Limulus*, develop in the form of simple depressions; the median eyes, on the contrary, have a complicated method of development, which apparently is very similar in the two forms.

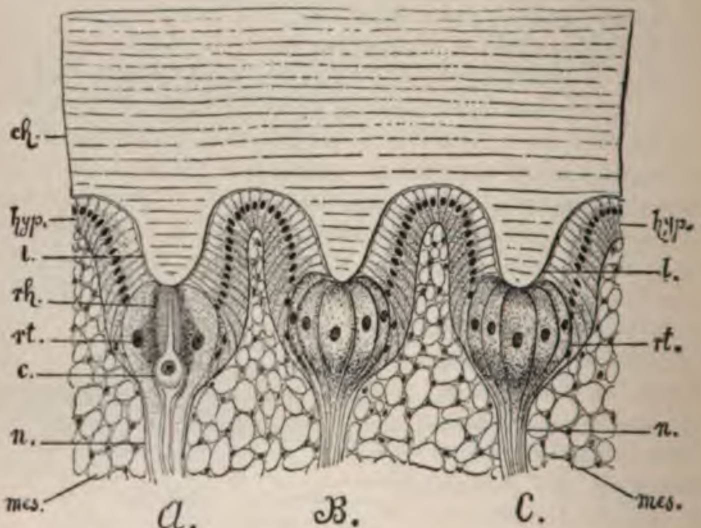

FIG. 37.—Three ommatidia of the lateral eye of *Limulus* (after WATASE). *A* is a median longitudinal section of the retinula, *B* and *C* show the retinulae in surface-view. *c*, central ganglion-cell; *ch*, chitinous cuticle; *hyp*, hypodermis; *l*, lenticular cone; *mes*, mesodermal tissue; *n*, nerve; *rh*, rhabdom; *rt*, retinula.

The *lateral eyes of Limulus* consist of a number of retinulae, each provided with a corneal lens (Fig. 37). The retinulae are continuous with the hypodermis, and each group might be regarded as a single eye, which has arisen in the way described above through the simplification of an ocellus-like eye. The lenses of the single eyes are only distinct from one another internally (Fig. 37, *l*); externally, they appear fused (*ch*). We might suppose that this process of fusion has gone still further in the lateral eyes of the Scorpiones, and has finally led to the formation of the common lens now found. In this view each lateral eye of the Scorpion is regarded as the sum of a number of single eyes. The rhabdoms contained between the retinal cells correspond to those in the eye of *Limulus*. The latter is somewhat highly developed, its character as a compound eye being recognisable from the formation of rhabdoms in the retinulae. The lateral eye of the Scorpion thus also appears as a degenerate facet-eye. The depression which ontogenetically represented it must therefore not be regarded as the primary optic pit.

In *Scorpio*, as is well known, there are several lateral eyes on each side. Each of these is to be considered as a complex of single eyes, and all taken together as representing a lateral eye of *Limulus*. They have, perhaps, been derived from one large facet-eye by the separation of individual complexes of single eyes. An altogether analogous process seems to occur in the Trilobites.

While the Trilobites usually have a facet-eye on each side, the genus *Harpes* has, in place of the facet-eyes, two or three prominences (*H. vittatus* 2, *H. ungula* 3, BARRANDE) with perfectly smooth surfaces, which are simple eyes, strongly resembling in outward appearance the lateral eyes of *Scorpio*. Palaeontologists have appropriately described them as ocelli, although, from a zoological point of view, they do not deserve this name, having most probably arisen in a way similar to that conjectured in connection with the lateral eyes of the Scorpiones.

Careful examination of the surface of Trilobite eyes perhaps allows of our forming further conclusions as to the origin of these facet-eyes, which coincide with the view just put forth. The whole surface of the facet-eye usually differs in its structure from the rest of the body covering. In some genera, however (*Phacops*, *Dalmania*, ZITTEL), the covering of the visual surface is identical with the rest of the shell, while the single lenses lie in rounded or polygonal depressions. This looks as if, in the last case, the single eyes were not close to one another, while in the first case they were crowded together. As our knowledge of the structure of the Trilobite eye is so small, this can merely be advanced as a conjecture.

The *median eyes of Scorpio*, by the distinct formation of retinulae and rhabdoms, are more evidently proved to be compound eyes. They are multilaminar (Fig. 10 *C*, p. 14). The same is the case with the median eyes of *Limulus*, the elements of which are also comparable with those of the eye of *Scorpio*. This multilaminar character raises the eyes under consideration to a higher ontogenetic level, further evidence of this being afforded by their complicated method of development. Both these characters make it impossible for us to trace back the median eyes of *Scorpio* and of *Limulus* to lateral eyes, although the two kinds of eyes otherwise show great agreement. Both the lateral and the median eyes of the Scorpion appear to be compound eyes, the one kind, however, showing more than the other a tendency towards the suppression of the distinction of the primary single eyes and towards the formation of one homogeneous eye. The fusion of eyes formerly distinct would, if we may follow this idea further, become continually closer, and finally lead to the formation of an eye in which the single eyes as such would be hardly recognisable or altogether indistinguishable. It does not appear to us possible that the eyes of the Araneae *have reached this stage*, although it will perhaps be considered paradoxical first to trace the evolution of the simple eye into the compound eye, and then to derive from this latter an eye which we are accustomed to claim as a simple eye.

The *eyes of the Araneae* show, especially in their manner of development, the greatest agreement with the eyes (median eyes) of the Scorpiones, apart from the fact that by their position they prove themselves to be homologous structures. The process of infolding so strikingly resembles the similar process in the Scorpiones, that we are obliged to consider the two as equivalent, and thus also to consider the Araneid eyes as more highly developed than their structure leads us to expect. The eyes of the Araneae are usually regarded as ocelli, and are compared with the ocelli of the Insecta. Their structure appears to justify this view, for the retina is composed of a continuous layer of similar cells (Fig. 38 *A* and *B*). The development of this layer is, however, more complicated than in the simple eye; in manner of formation it resembles the eye of *Scorpio* (Fig. 35, p. 65, and Fig. 10, p. 14). The multilaminar character is not, as in the ocellus, caused simply by the hypodermal layer pressing forward over the retina, but is the result of a process of infolding (Figs. 35 and 10). This striking resemblance to the eye of *Scorpio* alone inclines us to regard the Araneid eye as a *compound eye.** By the breaking-up of the retinulae, the uniform character of the retina would again be attained. There are besides, in the structure of the Araneid eye, certain indications which seem to support this view, and which would lead us to conclude that the retina is not composed of a uniform series of

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* [PURCELL (App. to Lit. on Opiliones, No. VI.) finds that the eyes of the Opiliones are three-layered inverse eyes, arising in a precisely similar way to the principal eyes of the Araneae and the median eyes of *Scorpio*. They contain *retinulae*, each composed of four cells surrounding a single rhabdom. PURCELL claims to have definitely proved that a retina composed of retinulae or of a modification of these occurs in the Opiliones and in the Araneae.—ED.]

single optic cells. According to GRENACHER, the rods in the eyes of all Araneids consist of *two parts*, and thus appear split longitudinally; in *Phalangium*, each rod is composed of *three parts*, and, in transverse section, has the shape of a trefoil. Although it is expressly asserted that the rods lie in the cells, we cannot avoid conjecturing that this bi- or tripartite character of the rods is perhaps a vestige of the rhabdom- and retinula-formation.*

The relations of the various pairs of Araneid eyes to one another are rendered difficult to understand by the differences in structure and development found in them. We are at first disposed to connect the anterior median eye with the median eye of *Scorpio*, and the other eyes with the lateral eyes of *Scorpio*. We cannot, however, reconcile with this view the fact that the posterior median eyes and the lateral eyes develop in almost the same manner as the anterior median eyes, while the lateral eyes of *Scorpio* form in a very simple way (Fig. 11, p. 17). We might therefore better trace back all the Araneid eyes to a breaking-up of the median eyes into separate complexes, such as has been assumed for the

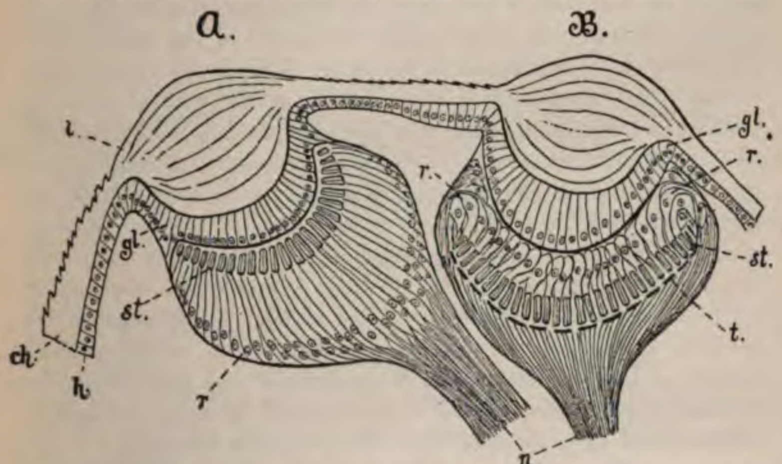

FIG. 38.—*A*, anterior, *B*, posterior median eyes of an Araneid (diagrammatic, after GRENACHER and BERTKAU). *ch*, chitinous cuticle passing into the cuticular lens (*l*); *gl*, vitreous body; *h*, hypodermis; *l*, lens; *n*, optic nerve; *r*, retina; *st*, rod; *t*, tapetum.

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* In the eyes of some Araneae (*e.g.*, *Atypus*), the vitreous body layer appears to be exceedingly thin. BERTKAU (No. 50) compares these eyes to the ocelli of the Insecta, and states that they obliterate the distinction between unilaminar and multilaminar eyes. Those ocelli with which these Araneid eyes are compared already show a vitreous body separate from the retina (in *Phryganea* and *Vespa*, GRENACHER), *i.e.*, the vitreous body and the retina no longer form one continuous layer. In this respect, these eyes have a structure similar to that of the Araneid eyes, and are removed from that of the unilaminar ocellus. According to the view adopted above, the median eyes of the Araneae, which so strikingly agree with the Insectan ocelli, must not be considered as homologous with the latter, but we must assume that this apparently similar development was brought about in different ways.

lateral eyes of *Scorpio.** In this case the lateral eyes would be altogether wanting in the Araneae. The differences in structure in the different pairs of eyes are, indeed, very remarkable; but, in the present state of our knowledge, it is not possible to explain them in a satisfactory manner.

In connection with the infolding of the Arachnid eyes and the secretion of the lens over that part of the fold which lies near the hypodermis (Figs. 35 and 10, p. 14), the elements of the retina undergo rearrangement. The part of the cells formerly turned outward is now directed inward. It carries the rods, as it also does even in the so-called accessory eyes (lateral and posterior eyes) of the Araneae (Fig. 38 *B*). The nerve-fibres become connected with the ends of the cells which were formerly turned inwards, but are now turned outwards. At these ends lie the nuclei of the retinal cells. This seems to be the definitive condition in the accessory eyes, and corresponds at the same time to the condition before infolding, apart from a few modifications that may still take place in the innervation (p. 67). It is otherwise with the so-called principal (anterior median) eyes of the Araneae and the median eyes of the Scorpiones. In the former, the rods lie at the outer (distal) ends of the retinal cells, while the nuclei lie internally (Fig. 38 *A*). The nerve-fibres join the nucleated proximal ends of the cells. This is also the case in the median eyes of the Scorpiones (Fig. 10 *C*). A displacement has therefore taken place here as a consequence of the infolding. The absence of this displacement in other Araneid eyes may perhaps be explained by the development of the tapetum by which the light is reflected back on to the ends of the rods that turn inwards.

The observations of KISHINOUYE and PURCELL quoted above, according to which inversion does not take place in the developing accessory eyes, again throw doubt on the manner of innervation of these eyes which has till now been considered likely, and lend probability to the repeated assertions that the nerve enters from behind.

From what is as yet known of the structure and development of the Arachnid eyes, we are not justified in doubting that displacement occurs. We have not, indeed, sufficient details of this process, which has been followed chiefly by MARK and PARKER, to be able to judge fully as to its occurrence. MARK has specially devoted his researches to the morphology of the process. In order to understand his view we must, however, briefly touch upon another theory concerning the origin of the Arachnid eye.

We derived the compound eyes of the Scorpiones and that of *Limulus* from more highly-organised (facet) eyes; another view, adopted specially by RAY

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* The recent statements regarding KISHINOUYE and PURCELL's observations (p. 68), according to which the anterior median eyes arise through inversion, while the other eyes do not, render highly probable the first conjecture that the former are to be traced back to the median eyes of the Scorpiones, and the latter to the lateral eyes of that animal.

LANKESTER, derives them from a simple eye (*stemma*, *ocellus*) by the grouping of the retinal elements into retinulae. The lateral eye of *Limulus* would, according to this view, represent a later stage in which a separation of the lenses has already taken place, which, progressing further, leads to the formation of facet-eyes. Although this view affords in some respects a satisfactory explanation of the different forms of the eyes, we were not able to accept it, because we could not find sufficient grounds for assuming that the continuous retina breaks up into separate groups.

The processes of development are more easily explicable by direct derivation of the Arachnid eye from the ocellus. The invagination then corresponds to the primary optic pit. If, however, we regard the eye as compound, as we did before, it then consists of the sum of the single eyes, and the invagination is not comparable with the primary optic pit, but must rather be considered as a secondary structure, which displaced the whole of the visual surface inwards in the form of an infolding, a process which, without further explanation, is incomprehensible. The process of inversion also then remains the same on the whole. The simpler case of the derivation from the ocellus is explained by MARK through degeneration of a part of the retina and greater development of the other part, the lens shifting meantime towards the latter (Fig. 39 *A*–*C*). The more highly developed portion of the retina comes to lie more and more beneath the lens (Fig. 39 *D* and *E*). While the nerves degenerate on the surfaces now turned outward, others become connected with the inner ends of these cells (*D* and *E*). The rods which lay originally behind the nuclei (*D*) are now found in

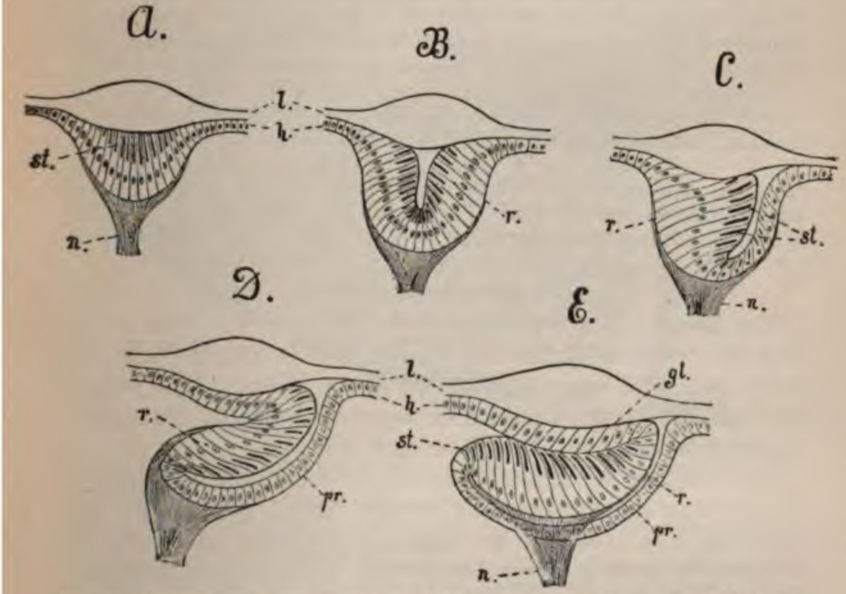

FIG. 39.—Diagrams illustrating the rise of the Arachnid eyes (chiefly after E. L. MARK). *gl*, vitreous body; *h*, hypodermis; *l*, lens; *n*, optic nerve; *pr*, post-retinal layer; *r*, retina; *st*, rods.

front of them (*E*). MARK regarded the spherical structures found behind the nuclei in the median eye of *Scorpio*, the so-called "phaospheres" of RAY LANKESTER, as remains of the original rods, while the rods now found in front of the nuclei (*E*, *st*) represent new formations. Since, however, the "phaospheres" are found in the lateral eyes of *Scorpio* which do not arise through inversion (RAY LANKESTER, CARRIÈRE) this view is not easy to maintain.

If we compare the two theories of the origin of the Arachnid eyes, we ought to take into consideration, as an important factor, that the compound (facet) eyes are built up on a convex base, while the Arachnid eyes have a concave base, and in this character more nearly resemble the simple eyes. This feature is wanting in the compound eyes of *Limulus*, which have as a base an almost level surface.

The attempt just made to bring the various Arachnid eyes into relation with one another was undertaken to reconcile the facts revealed by ontogeny with the structure of the adult eye. Physiological factors ought, perhaps, to have been taken more into account. It must be clearly understood that the above is merely an attempt to facilitate the comprehension of the Arachnid eyes, till, through further research, we have attained a more exact knowledge of their structure, and the ontogenetic processes through which they pass, which are still in many respects very obscure. The literature on this subject is so extensive, that we have not attempted to acknowledge the views of different authors in the way done in other parts of this work. It has thus been possible to treat our subject more freely.

The Respiratory Organs.

The Lungs. The two lungs of the Dipneumones arise in the form of two wide depressions at the bases of the limbs of the second abdominal segment (SALENSKY, BRUCE, MORIN). Their further development (SCHIMKEWITSCH, LOCY) somewhat resembles that already described for the lungs of the Scorpiones (p. 19).

The lung-sacs are directed forwards in relation to the stigmata. At the anterior end, especially in the ventral part of the sac, infoldings arise; these are the leaves (formation of the lung-book). The space between the two halves of each leaf is in direct continuity with the body-cavity, so that the blood freely enters the lung-leaves. The two lamellae are connected by cellular transverse trabeculae, no doubt arising from the mesoderm (LOCY); these are also present in the adult (Fig. 40), and are then said to be of a muscular character (MACLEOD). On the free surfaces of the leaves, *i.e.*, on those turned to the cavity of the pulmonary sac, a cuticle is secreted, which, on the surfaces directed ventrally, is homogeneous and of equal thickness, while on the dorsal surfaces it is stronger, and beset with small tooth-like thickenings (LOCY); this distinction between the two surfaces holds in the adult also (Fig. 40).

It has already been shown (Vol. ii., p. 358) that the lungs of the Arachnida show great morphological resemblance to the gills of the Xiphosura. KINGSLEY

(No. 61) points out in addition to this that the rudiment of the lungs in the Araneae so closely resembles that of the gills in *Limulus*, that the one might be mistaken for the other. Further, the rudiments of the gills in *Limulus* are somewhat sunk below the level of the ventral surface. The position of the developing lung at the posterior side of the limb is also of great importance. We are therefore disposed to regard the lungs of the Arachnids as modifications of once functional gills (Vol. ii., p. 358). When the gills are drawn into the body in such a way that the free posterior edge of the limbs, by its partial fusion with the body-wall, yields the stigma, the lower (true anterior) surface of the limb which lies close to the body must become the ventral body-wall of that region. This is in agreement with MORIN's statement, according to which the disappearing limb yields the outer covering of the lung. In such an origin of the lungs, it is clear that the lung-leaves arise chiefly from the ventral wall of the sac (posterior surface of the limb, Fig. 40). The lung-leaves correspond directly to the leaves of the gills which are still found in *Limulus*. We therefore refer the lung-leaves to the leaves of the gills, without assuming an invagination of the latter such as has been sometimes demanded (Vol. ii., p. 359). It has been stated that in such a phylogenetic origin of the lung-book we should expect to see the leaves appearing as projecting folds on the abdominal limbs, before the depression occurs, so that the lung-book would pass ontogenetically through a gill-stage. Such an ontogenetic stage does not occur, but the invagination takes place first, and the folds then form within it. It appears to us to be demanding too much to expect to find such an ontogenetic stage, and to be going too far to found an

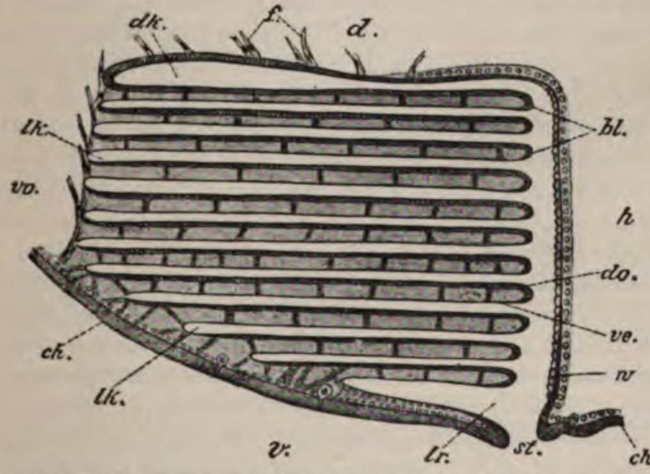

FIG. 40.—A somewhat diagrammatic longitudinal section through an Araneid lung (after MACLEOD). *bl*, lung-leaves; *ch*, chitinous covering of the body, and beneath it the cells of the hypodermis; *d*, dorsal side; *dk*, dorsal air-chamber; *do*, dorsal surface of a lung-leaf, provided with a thicker layer of chitin and teeth; *f*, fibres of connective tissue attached to the lung-sac; *h*, posterior side; *lk*, air-chambers; *lr*, common air-space of the lung-sac; *st*, stigmatic aperture; *v*, ventral side; *ve*, ventral surface of a lung-leaf with thinner and more even layer of chitin; *vo*, anterior side; *w*, posterior wall of the lung-sac, with the cellular matrix. Between the two lamellae of each lung-leaf (*bl*) the (darkly shaded) transverse trabeculae can be seen.

opposition theory, concerning the origin of the lung-books, upon its absence. Such a temporary retardation of one of the ontogenetic stages is here all the less improbable, since we have seen that even the gills of *Limulus* appear somewhat sunk in the ventral body-wall.

The most important evidence yielded by ontogeny in favour of a comparison of the Arachnid lungs with the gills of the Xiphosura is their common origin in connection with the abdominal limbs. Besides this, there is the striking agreement in the structure of the adult organs which has been specially pointed out by Ray Lankester and MacLeod, and the canal-like communication of the lung-sacs of the two sides which, to all appearance, finds its homologue in a similar connection between the gill-cavities on the two sides in *Limulus*.[*]

The Tracheae. If the pair of lungs in the Dipneumones arises from the second abdominal limbs, it must be assumed that the second pair found behind the first in the Tetrapneumones arises from the third pair of abdominal limbs. This pair, according to Morin's observations, disappears in the Dipneumones; but we may expect that further researches, made specially with this object in view, may reveal that it gives origin to the two tracheal trunks which are met with in most Araneids in addition to the lungs.[†] In a few Araneids (the genera *Dysdera*, *Segestria*, *Argyroneta*) the two stigmata of these tracheal trunks are found immediately behind the stigmata which lead to the lungs, and we can therefore hardly doubt that they are to be compared with the similarly-placed posterior stigmata of the Tetrapneumones. Where two stigmata (*Salticus*, *Micryphantes*), or, as is usually the case, a united pair of stigmata in the form of a transverse slit are found, immediately in front of the spinning mammillae, it might be assumed that the second pair of stigmata have been shifted back, just as the succeeding pair of limbs have been displaced backwards as the spinning mammillae to the posterior end of the body.

Taking the above facts into consideration, we are inclined to trace back the tracheae of the Araneae (and of the Arachnida generally) to lungs.[†] We assume that the air-chambers of the lungs lengthened out and extended far into the

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[*] [Simmons (App. to Lit. on Araneae, No. VIII.) finds that the lungs arise as infoldings on the posterior surface of the second pair of abdominal appendages, in the same way as the gills arise in *Limulus*, forming lung-leaves in the same way as the gill-leaves are formed in the latter. The lung-leaves, therefore, arise as an external structure on the posterior surface of the abdominal appendage; they sink in without any inversion or complication, in the way suggested by Kingsley. The tracheae develop on the third abdominal appendage; in their earlier stages, these appendages have, on their posterior surface, a folding similar to that on the second appendage. The author thus concludes that the lung-book condition is primitive and the tracheae derived from it.

See also Laurie (App. to Lit. on Scorpiones, No. IV.). This author is also in favour of MacLeod's view that the lung-books are to be derived from appendages whose lateral margins have fused with the ventral body-wall.—Ed.]

[†] [Purcell (No. VII.) derives the inner tracheal trunk from an entapophysis, the outer from the lung.—Ed.]

body, narrowing at the same time, so that the tracheal form was finally assumed. The flattened form of the tracheae in the Araneae seems further to support the view that they arose from the spaces between the lung-leaves. According to MacLeod, the air-chamber which lies most dorsally in the lung (Fig. 40, *dk*), and which is bounded by the wall of the lung-sac and the dorsal lamella of the uppermost leaf, usually differs in shape from the others, being more rounded, almost cylindrical in cross section, while the other chambers are narrow and slit-like. This air-chamber thus already approaches a trachea in form, and further resembles it in the structure of its wall, which is beset all round with chitinous teeth. We thus have a partial transition to the form of the trachea in the actual lung-sacs. The tracheae also show a great similarity to lungs in that the principal trunks of the two sides have, stretched between them, a connecting canal, such as is also present in the lungs, and which, in these latter, is of importance in comparing them with the gills of *Limulus*.

The process of the further distribution of the tracheae in the body was most probably determined by adaptation to a terrestrial existence, which led to the development of a respiratory system resembling the tracheal system of other air-breathing Arthropoda. It is well known that the tracheae of the Arachnida have repeatedly been regarded as homologous with the tracheae of other Arthropoda. The lungs were derived by those who held this view from tracheal tubes, which became flattened and much widened. Such a view seemed all the more justifiable, as the tracheae in the Arachnids also (Pseudoscorpiones, Solifugae, Opiliones, etc.) may be provided with a spiral thread, and may thus show a really striking agreement in structure with the tracheae of the Insecta, etc. We have already explained that we cannot accept such a view, but assume a separate origin for the respiratory organs of the Arachnida. It should further be mentioned that the tracheae of the Araneae have no spiral thread, but fine spines on their chitinous lining, these latter occurring in the same way in lungs. Another structural peculiarity which distinguishes the tracheae of the Arachnida from those of Insects, and which is also met with in lungs (Fig. 40, *f*), is found in the fine fibres of connective tissue which run out from the tracheae, and become inserted in other portions of the body. These are always said to be wanting in the tracheae of the Myriopoda and the Insecta (MacLeod, No. 10).

The co-existence of lungs and tracheae in the abdomen of the Araneae was regarded by Leuckhart (No. 8) as due to the relative amount of space in the anterior and posterior parts of the Araneid abdomen. The broad anterior portion of the abdomen admits of more massive development of the respiratory organs, while the elongation of the posterior part determines their greater length and wider distribution. There is here, therefore, only a partial transition to tracheal respiration, while in other Arachnida the tracheal system alone is developed.

E. The Spinning Glands and the Poison Glands.

The **spinning glands** arise as invaginations of the ectoderm on the fourth and fifth pairs of abdominal limbs, which are transformed into the spinning mammillae (Morin, Locy, Jaworowski). [These two pairs of abdominal appendages acquire, at an early period, a biramose form, each, like the primitive appendages of the Crustacea, consisting of an axis to which is attached an inner endopodite and an outer exopodite (JAWOROWSKI). Spinning glands may develop on both rays, and it is thus suggested that the primitive number of spinning mammillae was eight. No existing Spiders are known in which these eight mammillae are fully developed as functional organs; in *Liphistius* (POCOCK), however, the full number are present, but only the four external ones (exopodites) possess functional spinning glands. In the Dipneumones, we find present six functional mam-

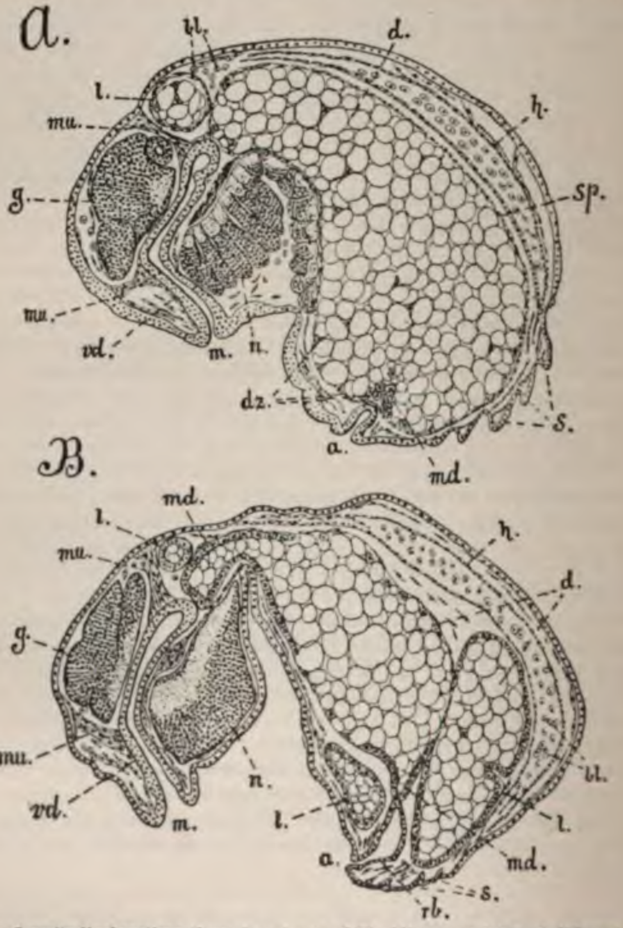

FIG. 41.—Longitudinal sections through embryos of *Theridium maculatum* at different stages (after MORIN). *a*, anus; *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk-cells; *g*, brain; *h*, heart; hepatic lobes; *m*, mouth; *md*, rudiment of the enteron; *mu*, muscles; *n*, ventral ganglia; *rb*, rectal vesicle; *s*, indication of external segmentation; *sp*, splanchnic layer of the mesoderm; *vd*, stomodaeum.

millae, the four large ones being derived from the exopodites of the fourth and fifth pairs of abdominal appendages, while the small intermediate mammillae are derived from the endopodites of the fifth pair, the endopodites of the anterior pair being either altogether wanting or else concerned in the formation of the *cribellum* or *collulus* (JAWOROWSKI, THORELL, POCOCK). Reduction appears to have gone furthest in the Tetrapneumones, where it is stated that only four spinning mammillae are present, possibly representing the exopodites and endopodites of a single pair of abdominal appendages. In all cases, the exopodites exhibit segmentation which is wanting in the endopodites. There can be no doubt that both structurally and developmentally the mammillae are true limbs.] The spinning glands themselves must, as already stated, be regarded as crural glands, and the same significance must be ascribed to the **poison glands,** which arise as ectodermal thickenings at the tips of the chelicerae and grow inward from that point (SCHIMKEWITSCH).

F. The Intestinal Canal and its Appendages.

The **stomodaeum** has already come under our observation as an invagination occurring early between the cephalic lobes, near their posterior margin (Fig. 28 *B*, p. 52). This invagination lengthens posteriorly (Fig. 41 *A* and *B*), and becomes differentiated into the pharynx, the oesophagus, and the sucking stomach. Strong muscle-strands, inserted upon the first and last of these, run to the body-wall (Fig. 41 *A* and *B*, *mu*). These are: a strand running from the pharynx to the dorsal part of the cephalo-thorax, another running from the sucking stomach in the same direction, and two lateral muscles extending from the latter to the edges of the sternal plates.

The **proctodaeum,** like the fore-gut, consists of several sections. It appears at a late stage, when the flexure-reversal is already far advanced, from an invagination of the last segment (Fig. 41 *A*, *a*), and grows forward; widening anteriorly, it gives rise to the rectal vesicle* (Fig. 41 *B*, *rb*), while a short posterior portion, the true rectum, remains tubular.

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* [The rectal vesicle, or stercoral pocket, usually regarded as a derivative of the proctodaeum, was stated by KISHINOUYE (No. 62) to arise from the mesoderm. Recently he has re-investigated this point, which, as he states, is inexplicable, and has been forced to the same conclusion. He finds in *Lycosa* and *Agalena* a maximum of fifteen pairs of mesoderm-segments and cavities: and just after the degeneration and fusion of the three posterior abdominal segments a new unpaired cavity appears in the mesoderm of the caudal lobe, and from this the stercoral pocket arises (App. to Lit. on Araneae, No. VI.). LAURIE finds in *Phrynus* (App. to Lit. on Pedipalpi, No. I.) that the stercoral pocket is derived from the enteron; he thinks that KISHINOUYE was misled by the involved condition of the entoderm in the Araneae. He agrees with this author that this organ does not arise from the proctodaeum.—ED.]

The **enteron** in the Araneae arises from the entoderm-cells which are distributed in the yolk. It begins to form at the posterior end of the body, and in this respect there is a resemblance to the Scorpiones; but a similar rudiment soon (or perhaps simultaneously) appears in the anterior part of the body (Fig. 41 *A* and *B*, *md*).

At a late stage of development, only a few days before hatching, there appears at the anterior end of the proctodaeum an accumulation of entoderm-cells (Fig. 41 *A*, *md*), which soon become arranged regularly at the periphery of the yolk to form an epithelium. There thus arises a trumpet-like structure, closed posteriorly and open anteriorly, which is the posterior part of the rudiment of the enteron (Fig. 41 *B*, *md*). A structure in all respects similar appears anteriorly at the blind end of the stomodaeum (*md*). This also arises from the yolk-cells, which have greatly increased in number. The enteron is completed when the two parts, which grow out towards each other with their wide-open ends, finally unite.

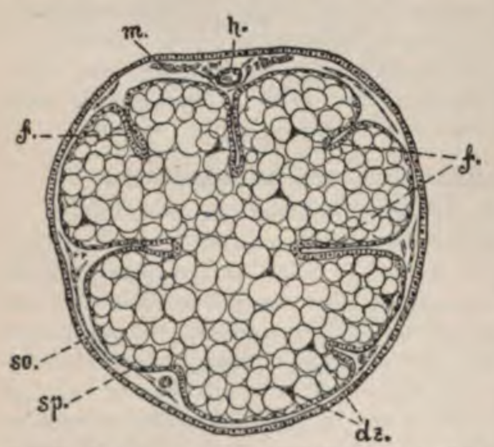

FIG. 42.—Transverse section through the abdomen of an embryo of *Pholcus phalangioides* (after MORIN). *dz*, yolk-cells; *f*, folds of the splanchnic layer; *h*, heart; *m*, muscles; *so*, somatic, *sp*, splanchnic layer of the mesoderm.

The stomodaeum and the proctodaeum then fuse with the enteron. But before this happens another more complicated structure, the liver, makes its appearance. Even before the development of the enteron began, a considerable number of folds (Fig. 42, *f*) appeared in the splanchnic layer of the mesoderm, which (in the absence of the entodermal epithelium) lay directly on the yolk. These folds grow into the mass of yolk, almost completely isolating certain complexes from the principal mass (Fig. 41, *l*). In these isolated yolk-complexes the formation of the epithelium is said to take place later in the same way as in the main mass itself, viz., by the yolk-cells coming to the surface, and becoming arranged in a regular layer (?) The epithelium thus formed now lies close under the splanchnic layer of the mesoderm. At the points where the isolated complexes remained connected with the principal mass of yolk, the efferent ducts of the liver arise. The lobed structure of the latter results from further bulgings of its wall. There appears to be some confusion regarding the origin of the caeca of the thoracic gut, they are probably entodermic (*cf.* p. 91). According to LOCY, these caeca of the stomach extend (in *Agalena*) into the bases of the limbs, a feature which would strikingly recall the Pantopoda.

The final shaping of the intestine does not take place until a late stage. When the Araneid hatches, the two principal rudiments of the enteron have not yet united; the chief part of the yolk is still present, and the young animal cannot therefore feed independently during the first part of its free life.

The formation of the intestine is treated in a somewhat similar manner by LOCY and by MORIN, whose accounts are also in general agreement with those of BALFOUR and SCHIMKEWITSCH. The few points on which these authors differ are not important. We must, however, devote some attention to an important appendage of the intestine, the so-called Malpighian vessels, as to the origin of which authors differ.

Two long tubular appendages of the intestine, opening into it almost at the point where the metenteron passes into the proctodaeum, are regarded as **Malpighian vessels.** In describing the formation of the proctodaeum, it was mentioned that it widens to form the rectal vesicle, also known as the cloaca. In *Agalena*, in which this point has been best investigated, the rectal vesicle lies dorsally, for the blind end of the enteron becomes connected with the ventral wall of the proctodaeum somewhat far back, so that the greater part of the vesicle lies in front of the junction of these two parts of the intestine. In *Theridium* and *Pholcus*, however, the enteron opens into the anterior end of the vesicle, if we may judge from MORIN's figures (Fig. 41 *B*). It appears to be very difficult, after the union of the enteron and the proctodaeum, to decide to which of these the different parts belong. This accounts for the different opinions of various authors as to the point at which the Malpighian vessels originate. While BALFOUR, SCHIMKEWITSCH, and MORIN state that they arise from the proctodaeum, LOCY and LOMAN consider them to be of entodermal origin. The statements of these last two authors are more definite than those of the other writers named above, the former having paid less special attention to this point.

LOCY states with considerable certainty that the Malpighian vessels arise from the tubular section of the posterior rudiment of the enteron, and LOMAN founds his decided opinion of their entodermal nature on the histological constitution of the intestine and the position of these vessels in the adult. We cannot, however, regard this point as fully established, although our own investigations made the entodermal character of the tubes appear highly probable.* Further, it has been definitely stated that the Malpighian vessels of the Scorpiones arise from the entoderm (p. 20), and we regard the statements made as to their ectodermal origin to be far less trustworthy.

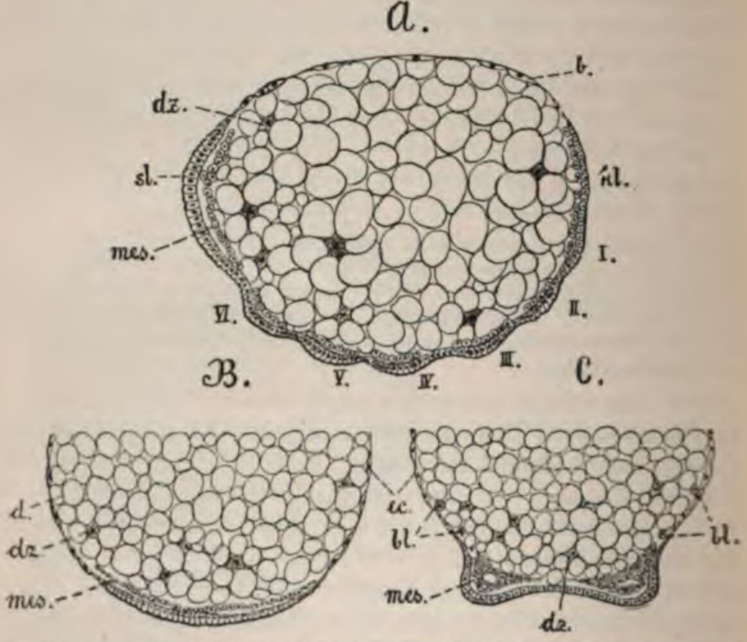

FIG. 43.—*A*, longitudinal sections. *B* and *C*, transverse sections through young embryos of *Theridium maculatum* (after MORIN). *b*, blastoderm; *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk-cells; *ec*, ectoderm; *kl*, cephalic lobe; *mes*, mesoderm; *sl*, caudal lobe; *I–VI*, first six segments.

The derivation of the so-called Malpighian vessels from mesoderm-strands, and that of the rectal vesicle from an unpaired coelomic sac belonging to the caudal region (KISHINOUYE, No. 62) are, from what we know of the manner of origin of these vessels, so improbable that we need not enter further upon it.†

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* In sections of young Araneids (*Tegenaria domestica*), which were kindly placed at our disposal by Dr. A. BRAUER, the formation of the intestine followed the course described above for *Agalena*; the posterior trumpet-shaped rudiments of the enteron had already opened ventrally into the proctodaeum. It appeared exactly as if the Malpighian tubes arose from an entodermal part, but this point can only be decided with certainty at a somewhat earlier stage when the enteron and the proctodaeum are not yet united. From the length of the tubes at the stages under consideration, we may conclude that their rudiment is to be found earlier.

† [See foot-note, p. 81.—ED.]

Should it be proved that the Malpighian vessels belong to the enteron, we should have another argument against a close relationship between the Arachnida on the one side, and the Myriopoda and Insecta on the other. The Malpighian vessels must then be regarded as resembling the appendages of the enteron in some Crustaceans, and could no longer be compared with the synonymous vessels in the Insecta.

The Mesodermal Structures.

The still unsegmented germ-band (Fig. 23 *C*, p. 46) becomes distinguished from the rest of the blastoderm partly by the cylindrical nature of the ectoderm-cells, and by the growth of the subjacent mesoderm-layer. This latter is at first a continuous band, which, as a single layer, occupies the whole area of the germ-band (Fig. 43 *B*). It, however, soon becomes multilaminar by active increase of its cells, and now undergoes differentiation into two mesoderm-bands divided by a slit, which appears along the middle line (Balfour, Locy). This occurs at a time when the germ-band externally shows division into six segments (Fig. 25 *A*, p. 48, and Fig. 43 *A* and *C*). The external segmentation seems to precede internal segmentation; this latter, however, soon takes place, the mesoderm-bands breaking up into the primitive segments in which the segmental cavities appear (Fig. 43 *A* and *C*). Spaces, entirely free from mesoderm, occur between the consecutive primitive segments (Schimkewitsch, Morin, Fig. 43 *A*). In the cephalic region, and especially in the caudal region, where the differentiation of the mesoderm into primitive

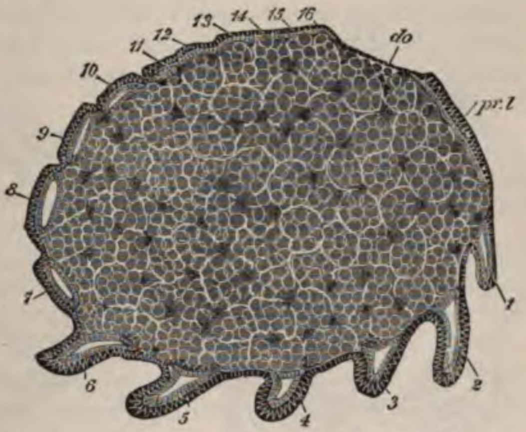

Fig. 44.—Longitudinal section through an embryo of *Agalena labyrinthica*, somewhat at the same stage as in Fig. 27 (after Balfour). The section is taken slightly to one side of the middle line to show the extension of the primitive segments into the limbs. In the centre is the yolk with the yolk-cells. *do*, the small portion of the yolk not covered by the germ-band; *pr.l*, cephalic lobe; *1–16*, the body-segments; *1*, chelicerae; *2*, pedipalps; *3*, first pair of legs, etc.

segments occurs last, the two mesoderm-bands are connected. Differentiation takes place from before backward, except in the most anterior segments, which, as already mentioned, in the Araneae as well as in the Scorpiones, become distinct somewhat later than the following cephalo-thoracic segments. The number of the primitive segments corresponds to that of the body-segments, one pair of the former occurring in each of the latter. The cephalic lobes also contain pairs of primitive segments, as the descriptions of **Balfour**, **Morin**, and **Kishinouye** undoubtedly show. Here, again, we have a resemblance to the Scorpiones (Fig. 13 *A*, p. 22). In the cephalo-thorax and also in the abdomen, as far as the latter possesses appendages, the primitive segments extend into the limbs; indeed for the time they withdraw almost entirely into the limbs (Figs. 44 and 45 *A*). The mesoderm-bands naturally also take part in the displacement undergone by the two halves of the germ-band in consequence of the pressing forward of the yolk-mass to the ventral side. Whereas they formerly lay near the ventral median line (Fig. 43 *C*) they now appear removed from it, and divided by the so-called yolk-sac (Fig. 29 *A*, p. 53). The segmental cavities

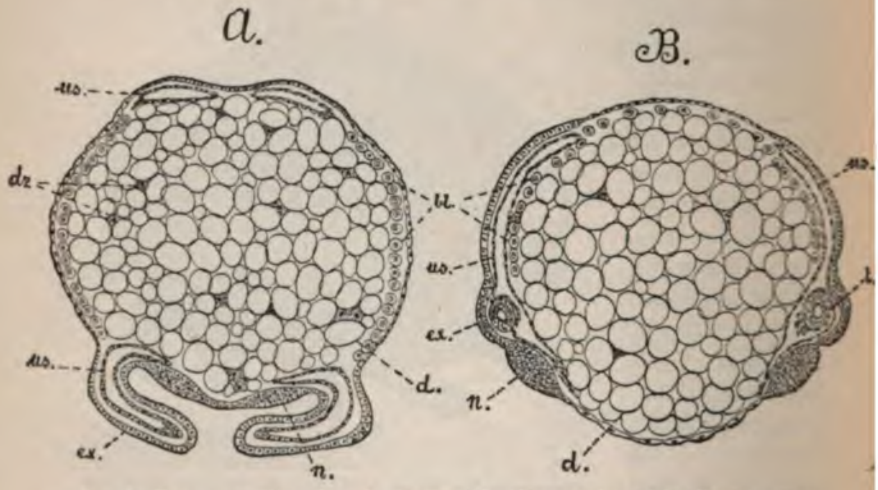

Fig. 45.—Transverse sections through embryos of *Theridium maculatum* (after **Morin**). In *A*, the embryo, which is curved round the yolk, is cut through twice; the thoracic limbs and primitive segments can be recognised below, while the abdominal primitive segments are seen above. *B*, cross-section through the abdomen of an older embryo, in which the primitive segments have increased in size. *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk-cells; *ex*, limbs; *l*, lung invaginations; *n*, rudiment of the chain of ganglia; *us*, primitive segments.

increase considerably in size, the primitive segments extending towards the dorsal side (Fig. 45 *B*). This process exactly corresponds to that we have already met with in the formation of the coelom in the Annelida (Vol. i., p. 289).

The following are the derivatives of the primitive segments:—

1. The somatic layer gives rise to the body-musculature (as thickenings near the ventral middle line of the abdomen), the two strong longitudinal muscles being specially noteworthy, and also to the subcutaneous connective tissue. According to SCHIMKEWITSCH, the endoskeleton also is derived from the somatic layer, but this statement we give with reserve. The covering of the parts arising through invagination of the ectoderm (stomodaeum and proctodaeum, lungs, glands), together with their musculature, thus the strong musculature of the stomodaeum, already mentioned, is also derived from the somatic layer.

2. The splanchnic layer gives rise to the covering of the enteron, the blood-vascular system, and the genital organs.

The coxal glands are probably related to the mesoderm and coelom, as in the Scorpiones (pp. 24 and 92), [*cf.* BRAUER and PURCELL].

G. The Blood-vascular System and the Body-cavity.

The Blood-vascular System. At a time when the limbs have already developed, there appear, above the primitive segments, between the ectoderm and the yolk, large round cells (Fig. 45 *A* and *B*, *bl*), concerning whose origin there is considerable difference of opinion.

BALFOUR derived these cells from the yolk-cells. To the latter he also traced the origin of the dorsal mesoderm (Fig. 29, p. 53). This last assumption was refuted by SCHIMKEWITSCH, LOCY, and MORIN, who agree in stating that the primitive segments extend to the dorsal middle line. The cells which, at later stages (Fig. 29), are found dorsally, as in Figs. 45 *B* and 46, therefore belong to the primitive segments. But, besides these, there are the large round cells mentioned above (Fig. 45 *A* and *B*, *bl*), and with regard to their origin, SCHIMKEWITSCH and LOCY agree with BALFOUR, deriving them from the yolk-cells. KISHINOUYE has recently adopted the same view, which seems in accordance with the constitution of these cells. They are much larger than the cells of the primitive segments (Fig. 45 *A* and *B*); we might, nevertheless, like MORIN, derive them from these, and assume that they had separated from the primitive segments in an early stage, when the cells of these segments were themselves larger. Better nourishment near the yolk as the cells increased in number would also determine increase in size. This view is further supported by the fact that they are found in the cavities of the primitive segments (SCHIMKEWITSCH). This latter author, indeed, thinks that they reach these cavities from the yolk by breaking through the wall of the segment, but this view seems improbable.

So long as the origin of the isolated cells lying between the ectoderm and the yolk is not definitely established, we may regard them as mesoderm-cells, and we are especially inclined to consider them as derivatives of the yolk-cells from a comparison with similarly related cells found in the Vertebrata, which are there undoubtedly derived from the yolk. These isolated cells eventually become blood-corpuscles. They collect dorsally during the upward growth of the primitive segments (Fig. 45 *B*), and, as they press somewhat closely against one another, they form (especially in the abdomen) a compact strand of cells which prevents the junction of the primitive segments in the dorsal middle line (Fig. 46, *bl*). Subsequently the mesoderm grows between this strand and the ectoderm, and thus the two primitive segments meet to form a partial dorsal mesentery. At a later period, the walls of the primitive segments grow between the yolk and this strand of cells, and unite with one another below the latter (Figs. 46 and 47 *A*). This strand of cells has consequently become enclosed by a layer of mesoderm having the form of a longitudinally-placed tube, which is at first attached to the somatopleure above and the splanchnopleure below. The tube soon loses its connection with its parent mesoderm (Fig. 47 *B*), and we now find a continuous layer of mesoderm (somatopleure) lining the ectoderm, while another layer covers the yolk (splanchnopleure); between these two layers is the body-cavity, in which the mesodermal tube now lies freely. This tube is the heart, and, so far as can be judged, it is formed directly from the walls of the primitive segments (SCHIMKEWITSCH, LOCY, MORIN (Fig. 47 *A* and *B*)). As a consequence of the development of the heart, the primary continuity of the cell-elements of the primitive segments becomes interrupted at this point (Fig. 47 *B*).

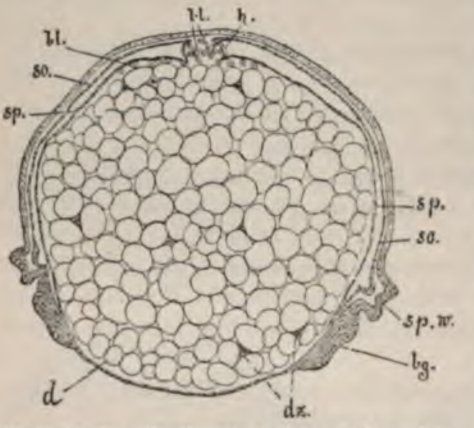

FIG. 46.—Cross-section through the abdomen of an embryo of *Pholcus phalangioides* (after MORIN). *bg*, ventral chain of ganglia; *bl*, blood-corpuscles; *d*, yolk; *dz*, yolk cells; *h*, heart; *so*, somatic, *sp*, splanchnic mesoblast; *sp.w*, spinning mammillae.

(Compare with the development of the heart in the Annelida and in the Mollusca.)

The isolated cells which had become grouped together into a strand become blood-corpuscles. Their crowded condition and their extremely close connection with the walls of the primitive segments suggested the idea that the heart was derived from a solid mesodermal strand extending along the dorsal middle line (BALFOUR), but this view cannot be verified; the formation of the heart may be directly compared with the similar process in the Annelida. The cavity of the heart corresponds to a *part of the primary body-cavity*, enclosed on each side by the primitive segments.

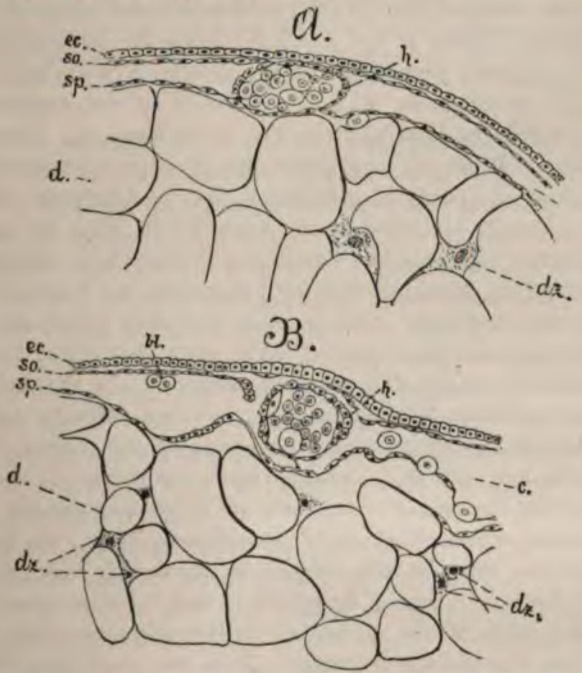

FIG. 47.—Transverse sections through the abdomen of embryos of *Theridium maculatum*, showing the formation of the heart (after MORIN). *bl*, blood-corpuscles; *c*, coelomic cavity; *d*, yolk; *dz*, yolk-cells; *ec*, ectoderm; *h*, heart; *so*, somatic, *sp*, splanchnic mesoblast.

The heart lies in a depression of the yolk (Fig. 47 *B*). The latter is covered only by the splanchnic layer of the mesoderm, as the entodermic epithelium is still wanting. From this part of the splanchnopleure, a mesodermal lamella is said to separate and grow round the heart to form the pericardium (SCHIMKEWITSCH). The alary muscles of the heart are then formed from the somatic mesoblast. The pulmonary veins arise as outgrowths of the pericardium, while the anterior and posterior aortae, as well as the lateral arteries, originate as prolongations of the heart or as outgrowths from it (SCHIMKEWITSCH).

While the cavity of the heart appears to be a part of the primary body-cavity, the pericardial space, according to SCHIMKEWITSCH, corresponds to a part of the secondary body-cavity. The pericardium in the Arachnida forms a tube, and is not comparable with the synonymous structure in the Insecta. But before we can make any definite statement as to the nature of the pericardium we must have a more exact account of its origin.

The Body-cavity. In the Arachnida, as in other Arthropoda, the blood-vascular system is not separated from the body-cavity, but the latter is directly connected with the circulation of the blood. The method of development of the body-cavity in the Arachnida is, however, strikingly different from that in the Crustacea, Myriopoda, and Insecta. While, in these latter, the primitive segments are not large and soon undergo degeneration, in the Arachnida they are almost as largely developed as in the Annelida (Figs. 45 and 46). The primitive segments are also highly developed in *Peripatus* to begin with (Fig. 100), but this form resembles the Insecta in that the segments very soon cease growing, and after a rich growth of cells undergo early disintegration. The adult body-cavity forms (as a pseudocoele) outside the primitive segments. In the Arachnida it forms somewhat differently; it is, however, difficult, from the statements before us, to arrive at a satisfactory judgment, since little stress has until now been laid upon this point. It is certain, however, that the primitive segments are of *considerable size even at a somewhat advanced stage of development* (Figs. 46 and 47). Between the somatic and splanchnic layers of each primitive segment there is a rather large cavity, and we must assume that when the union of the segmental cavities takes place this passes direct into the adult body-cavity. It is true that here, also, the body-cavity would not retain the coelomic epithelium up to the last, but the wall of the primitive segments would also break up (Figs. 47 *A* and *B*, 41, p. 80, 42, p. 82), yielding the muscular and connective tissue elements, so that at last, in the Arachnida, a condition would be reached similar to that attained at a much earlier stage in the development of the Crustacea, Myriopoda, and Insecta.

The segmentation of the mesoderm begins to disappear when the primitive segments have grown to a considerable size and the embryo itself is near the stage illustrated in Fig. 27. The segmental cavities unite in the cephalo-thorax and the dividing walls (dissepiments) gradually disintegrate, the cells falling into the body-cavity (Schimkewitsch). These cells probably give rise to blood-corpuscles. The primitive segments of the cephalic lobes seem already to have fused with those of the cheliceral segment, at least Schimkewitsch speaks of a connection between the two which, however, he explains in another way.

If we understand Schimkewitsch rightly, he assumes that the pair of primitive segments in the cheliceral segment arise by division from the pair in the head; we should be more inclined to assume the opposite of this, *i.e.*, an extension of the first trunk-segment into the cephalic region. It, however, appears from the accounts and figures before us that the cephalic and cheliceral segments undoubtedly have separate primitive segments. A union of these two pairs of segments, like that described by Kleinenberg for *Lumbricus*, would then take place.

The two segmental cavities of the head become united; such a union of the cavities of the two sides must take place in the trunk also as a result of the processes described in connection with the formation of the heart (Fig. 47). This at least applies to the dorsal side; on the ventral side, the primitive segments are at first still far apart (Fig. 46), but they shift gradually towards the middle line, so that they finally extend round the whole mass of yolk. In the abdomen the primitive segments remain separate longer, a fact which is in keeping with their later differentiation. Even when they are fused together, the mesoderm represents two extensive layers passing into one another—an outer or somatic layer and an inner or splanchnic layer; between these is the secondary body-cavity (Schimkewitsch).

From the splanchnic layer, the folds already mentioned in connection with the formation of the intestine grow into the yolk (Fig. 42, p. 82), in this way cutting off from it isolated masses which correspond to the later hepatic lobes. We should like here to draw special attention to the important fact that the yolk is so long a time bounded solely by mesoderm (Figs. 46 and 47), and that the epithelium of the enteron develops very late (Fig. 41, p. 80); indeed, the mapping out of a large part of the enteron, that of the liver, seems to be commenced by the mesoderm.

Whether the distribution of these folds corresponds to a true segmentation appears doubtful, although this might be indicated by the appearance of four lateral folds in the cephalo-thorax. It appears that these correspond to the thoracic caeca of the enteron (?), for in the abdomen also a number of folds occur, and it is these principally that give rise to the form of the liver (Morin). The folds which penetrate the yolk not only come from the side, but from above and below, and thus represent oblique as well as longitudinal layers

(Schimkewitsch), so that it is impossible to trace them back, as Balfour attempted to do, to the partition walls of the somites.

A structure resembling the fat-body of the Insecta which is present in the body-cavity (Ray Lankester's lacunar blood-tissue) is, according to Schimkewitsch, formed, like some of the blood-corpuscles, out of the yolk-cells which immigrate into the body-cavity, and these cells also are said to become arranged into a "peritoneal" layer, which envelops the internal organs. In both cases we should, after what has already been said, feel disposed to derive these structures from the mesoderm, *i.e.*, from the primitive segments, although such a derivation would have to be established by further researches. Where a peritoneum is present, it would be of interest to learn its relation to the primitive coelomic epithelium.

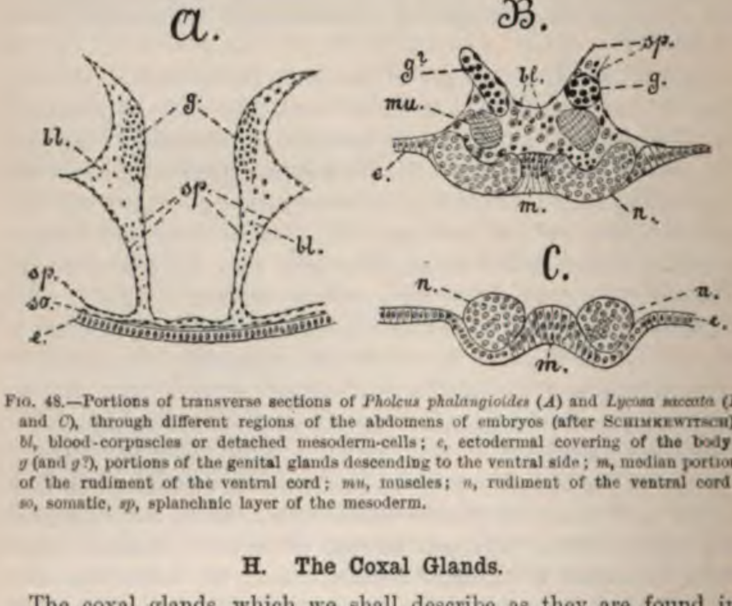

Fig. 48.—Portions of transverse sections of *Pholcus phalangioides* (*A*) and *Lycosa saccata* (*B* and *C*), through different regions of the abdomens of embryos (after Schimkewitsch). *bl*, blood-corpuscles or detached mesoderm-cells; *e*, ectodermal covering of the body; *g* (and *g*?), portions of the genital glands descending to the ventral side; *m*, median portion of the rudiment of the ventral cord; *mu*, muscles; *n*, rudiment of the ventral cord; *so*, somatic, *sp*, splanchnic layer of the mesoderm.

H. The Coxal Glands.

The coxal glands, which we shall describe as they are found in the already hatched Araneid, show great resemblance to those of *Scorpio*, and no doubt arise in the same way as in that animal. An actual efferent duct has for the most part only been proved to exist in young Araneids, where it opens at the base of the fifth pair of appendages (Bertkau, No. 51). In the young of *Atypus*, Bertkau found, on the anterior pairs of limbs, *i.e.*, third and fourth pairs of appendages, slits corresponding in appearance and position to the apertures of the coxal glands on the fifth pair, and this led him to conclude that there were originally several pairs of these glands.

KISHINOUYE's derivation of the coxal glands from an ectodermal invagination which lengthens into a tube is not only incompatible with their origin in the Scorpion from the mesoderm (p. 24), but also with their relation to the body-cavity. According to KISHINOUYE's own statement, the tubular rudiment of the coxal gland opens at its inner end *in the shape of a funnel into the coelom*, so that the accepted view that these glands are nephridia is confirmed, provided the accounts given are correct. If these glands are ectodermal in origin, then they must be regarded, not as coxal, but as crural glands, and we would expect them to end blindly. STURANY (No. 14), the most recent investigator of the coxal glands in the Arachnida, considers them to be nephridia. If his conjecture that they end in a terminal sac as in the Crustacea proves correct, the latter would no doubt correspond to a part of the body-cavity. We refer the reader to our account of the coxal glands in the Scorpiones (pp. 24 and 87).

I. The Genital Organs.

According to SCHIMKEWITSCH, the genital organs arise in the anterior part of the abdomen, within the two longitudinal folds of the splanchnic layer, which have risen up into the yolk from the ventral side. In the median layer of each of these folds an ovoid thickening appears (Fig. 48 *A*). This consists of large central and flat peripheral cells, the latter representing an enveloping epithelial membrane (Fig. 48 *B*). The anterior end of the rudiment curves round towards the ventral side, and is said to correspond to the efferent ducts, while the rest represents the germ-glands. When the young Araneid hatches, there is still no communication between the efferent ducts and the exterior; this is established later by means of an ectodermal invagination (SCHIMKEWITSCH).

[PURCELL (App. Lit. on Araneae, No. VII.) traces the ducts to tubular growths of the abdominal mesodermal segments; the openings of these ducts into the coelom become connected with the genital cells which grow forward from the posterior end of the germ-band. Similar structures develop in all the abdominal appendages, but only those on the second segment persist. He regards them as modified nephridia.]

VII. Acarina.

Oviposition. The majority of the Acarina lay eggs, a few (*e.g.*, *Halarachne*) are said to be viviparous. Some (*e.g.*, *Scutovertex*) appear to be viviparous at certain times of the year and ovo-viviparous during the remainder of the season, others are habitually ovo-viviparous. The Acarid egg is surrounded by a more or less strong shell, sometimes covered with prominences; in many species this protective shell is extremely thick and traversed by fine pore-canals.* The eggs are deposited in various places, according to the

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* [According to TROUSSART (App. to Lit. on Acarina, No. VII.), the female of *Syringobia chelopus* among the plumicolous *Sarcoptidae* at times reproduces parthogenetically; the eggs thus produced in the absence of males have no shells.—ED.]

habits of the parent. They are found in decaying wood, in damp earth, on the under surfaces of stones, in dung-heaps, on leaves, fruit, etc. Some, but by no means all, parasitic forms lay their eggs on or in the body of the host. The eggs are at times laid in a heap, at other times separately; in the latter case they are often stalked; those of *Myobia musculi* have a process at the posterior pole by which they are attached to the fur of the mouse. According to **Haller**, many *Oribatidae* carry their eggs attached to their backs, others are said to lay them in a part of their cast-off chitinous integument.* The form of the eggs is most commonly elliptical (Fig. 50), sometimes oval, and more rarely globular (Fig. 49), or even discoidal. For their size, they are richly provided with food-yolk.

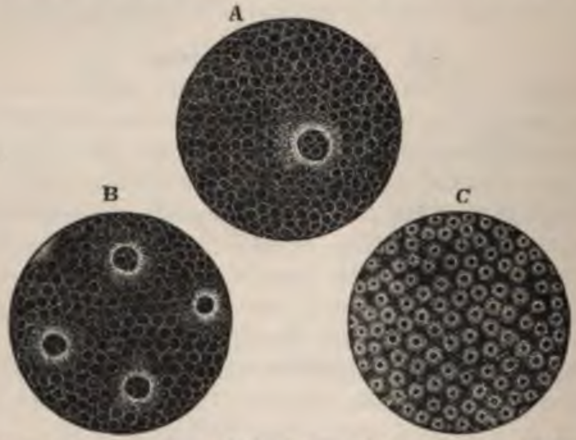

Fig. 49.—Cleavage and formation of the blastoderm in the egg of *Tetranychus telarius* (after Claparède, from Balfour's *Text-book*). The yolk-granules are represented by clear circles (in *A* and *B*). The nuclei, with the clear areas of protoplasm around them, are much larger than the granules. *C*, an egg in the stage of blastoderm-formation.

1. Embryonic Development.

The embryonic development in these eggs is difficult to follow on account of their minute size, and is therefore not well known.

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* [Neither of these assertions is quite correct. The carrying of the eggs is almost entirely confined to the genus *Damaeus*—it is most commonly the immature individuals, not the adults, which pile the eggs on their backs; it is manifest that at this period they cannot have any eggs of their own to carry. What happens is that the larvae are born with soft abdomens, and have the instinct of piling upon their backs dirt, rubbish, etc., as a protection; they will pick up and carry the eggs and empty egg-shells, from which they may themselves have emerged, but they will equally pick up and carry the eggs of other Acarina. The statement concerning the eggs being found in the cast integument has never been confirmed, and is very doubtful.—Ed.]

CLAPARÈDE's account (No. 77) is still the most complete.* According to this writer, in *Tetranychus telarius*, the nucleus, surrounded by formative protoplasm, rises to the surface of the yolk (Fig. 49 *A*) and soon divides. Repeated division (Fig. 49 *B*) gives rise to a large number of nuclei, each surrounded by an area of protoplasm. The nuclei remain lying at the surface of the egg, and by increasing still further in number, they, with the protoplasm around them, give rise to the blastoderm (Fig. 49 *C*).

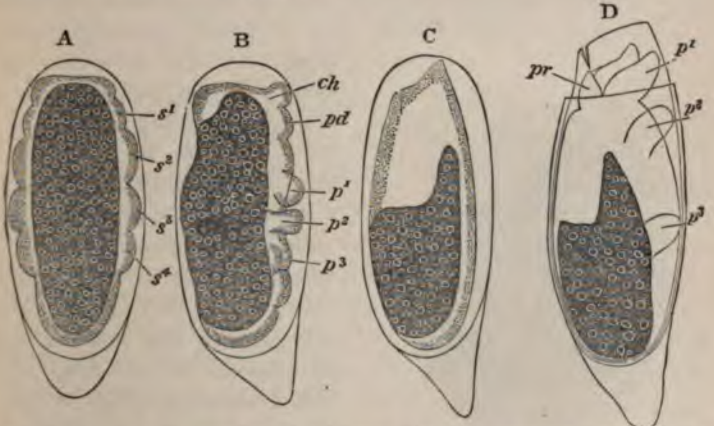

FIG. 50.—Embryonic development and formation of the first larval integument in *Myobia musculi* (after CLAPARÈDE, from BALFOUR's *Text-book*). In *D*, the egg-integument has split, and the embryo, surrounded by the first larval integument, is in the act of leaving the egg. *ch*, chelicerae; *pd*, pedipalps; p^1–p^3, the first three pairs of limbs; *pr*, proboscis (which has arisen through the fusion of the chelicerae and the pedipalps); s^1–s^4, four post-oral segments. The yolk is represented by the darker area.

According to ROBIN and MÉGNIN (No. 104), total cleavage occurs in the eggs of the *Sarcoptidae*. The egg, while still in the oviduct, was seen to break up into four cleavage-spheres. This, if correct, reminds us of the condition described in the Araneid egg, which, however, does not there lead to the complete division of the egg into cleavage-spheres. Total cleavage is said to be undergone also by the egg of *Chelifer* (p. 28), and the same has been maintained, at least at a later stage, of the eggs of the Opiliones also (p. 32).

The blastoderm was examined in a number of Acarina, and always consisted of a thin single layer of cells enclosing the yolk. As it develops further, thickenings take place at points corresponding to the future ventral surface, especially in the cephalic and caudal regions. The germ-band thus arises here (Fig. 50 *B*) in the same way as in other Arachnids. At first it is an equally thickened

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* [HENKING's account is perhaps more correct.—ED.]

band, but later it breaks up into two symmetrical halves, a ridge of yolk pressing outwards in the median line. Here also there is agreement with the Araneae. The germ-band soon becomes segmented (Fig. 50 *A*). The cephalic lobe, which, in *Myobia* as in the Araneae, curves over to the dorsal side (Fig. 50 *B*), and the caudal lobe become segmented off from the trunk. The part lying between them, which corresponds to the cephalo-thorax, is divided up into a number of segments, the truncated rudiments of the mouth-parts and limbs soon appearing on these (Fig. 50 *B*). This segmentation is less distinct in other Acarina, and, as is well known, eventually disappears. The abdomen is still comparatively large in such an embryo; in many Acarina it is much reduced, or is united to the cephalo-thorax.

Fig. 51.—Embryo of *Atax Bonzi* surrounded by the deutovum and the egg-shell (after Claparède). *ch*, chelicerae; *d*, yolk; *dm*, deutovum; *ch*, egg-shell; *kl*, cephalic lobe; p_1-p_3, the three pairs of limbs; *ped*, pedipalps; *sl*, caudal lobe.

Before development has progressed thus far, a delicate structureless integument separates, in *Atax*, from the embryo, and surrounds it, like a second egg-integument, in the form of a closed envelope (Fig. 51, *dm*). In other Acarina, this process only takes place later, when the limbs are already present, so that these are found on the envelope in the form of sheaths surrounding the actual limbs (Fig. 52, *dm*). This delicate envelope, though separated from the embryo, is thus seen to be a true larval integument.

The embryo is now enclosed in a double envelope, and the dorsal surface which, up to this period, showed little signs of development, being covered only by a thin cell-layer, now commences to develop by the growth of the mesodermal elements towards this surface. The yolk for some time longer retains its former appearance (Figs. 50–53), but we must no doubt assume that the formation of entoderm has already begun. Nothing certain is as yet known of the development of the germ-layers and the rudiments of the organs in the Acarina. The limbs of the embryo lengthen (Figs. 51 and 53 *A*) and become segmented (Fig. 52). In the stage depicted in Fig. 51, and more especially in the following stages, the embryos of many

Acarina show great resemblance to those of the Araneae (Figs. 51 and 57 *A*). The chelicerae and pedipalps unite to form the proboscis (Fig. 53).* The abdomen (in *Atax*) now decidedly preponderates over the anterior part of the body (Fig. 53). There are only three pairs of limbs when the embryo breaks through its envelopes and begins free life (Figs. 51–53, p_1–p_3). We thus find, in the Acarina, a larval stage with *only three pairs of limbs*, as distinguished from the four pairs of the nymph and of the adult, which, in other points of both outer and inner organisation, the embryo greatly resembles.†

2. The Formation of the Larval Integuments and the Further Course of Development.

It was mentioned that, in many Acarina, *e.g.*, *Atax*, the embryo casts off a cuticular integument at an early stage when the limbs have not yet developed or are only indicated. CLAPARÈDE's *deutovum* is thus produced, the embryo within the egg-shell thus becoming enclosed in a second envelope (Fig. 51). The resemblance of the "deutovum" with the embryo enclosed in it to an intact egg is increased by the fact that, after casting off the primary egg-shell (*eh*), the embryo undergoes further changes in its external form within the deutovum. In *Trombidium* and *Myobia* this cuticular membrane is cast only after the rudiments of the limbs have appeared (Fig. 52). In *Trombidium*, this membrane is provided with appendages which surround the limbs like sheaths (HENKING), but this is not the case in *Myobia*. Here the limbs form in the usual way (Fig. 50 *B*), but when they have grown to a considerable length they become applied to the ventral surface of the body, and gradually become flattened to such a degree as hardly to project from the surface of the body. The whole embryo is once more oval and apparently devoid of appendages (Fig. 50 *C*). At this stage a cuticular membrane becomes detached from the embryo, bearing near its antero-dorsal extremity (in the nuchal region, according to CLAPARÈDE) a tooth-like structure, composed of two thin chitinous processes closely applied to one another. This structure is not well depicted in Fig. 50 *C* and *D*,

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* [This is true of the forms described by HENKING, but by no means holds good for all the Acarina, in the majority of which the chelicerae remain as perfectly distinct and movable organs.—ED.]

† [In the *Phytoptidae* the adult has only two pairs of legs. The larvae and nymphs do not always resemble the adults in other respects, for instance, in the *Oribatidae*, they differ essentially in external appearance, and the adult has a well-developed tracheal system which is entirely wanting in the larva.—ED.]

where it appears more like a slit (at the left side of the inner envelope). CLAPARÈDE thought that the tooth served for splitting the envelopes. It thus performs the same function as the egg-tooth of the Araneae (p. 58), but it need hardly be pointed out that the difference in position of the two structures makes it impossible to homologise them. We might rather compare the structure just described with the egg-tooth of the Opiliones (p. 33).

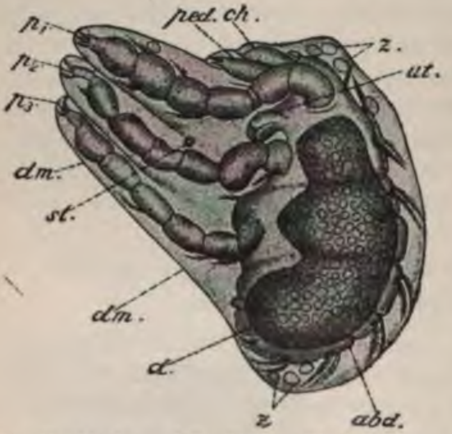

FIG. 52.—The larva of *Trombidium* with six limbs, enclosed in the deutovum (after HENKING). *abd*, abdomen; *ch*, chelicerae; *d*, yolk (enteron); *dm*, deutovum; p_1-p_3, first to third pair of limbs; *ped*, pedipalps; *st*, "stigma"; *ut*, "primitive trachea"; *z*, isolated cells beneath the deutovum.

The embryo, surrounded by the cuticular membrane, emerges from the egg-shell (Fig 50 *D*), which, however, continues to surround the greater part of it. This recalls the cuticular membrane in the Araneae, which forms under the egg-shell and encloses the hatched and still motionless embryo. The limbs now grow out again, but are reduced as before, and a second cuticular integument is cast off, so that the greater part of the egg is enclosed by two integuments as well as by the egg-shell. The *tritovum* of CLAPARÈDE is thus formed. Within it the embryo attains the six-limbed form in which it finally emerges.

In the secretion of two envelopes within the egg in ***Myobia*** we have a specially complicated process. So far as is known, only one such envelope usually forms in the egg (Fig. 51). We must probably regard the formation of these envelopes as a very early moult, which no doubt originally took place during larval life. This view is supported by the fact that, in the further course of development, several similar moults occur. The embryo may also actually leave the egg surrounded by this first larval integument. In *Myobia*, *Damaeus*, etc., the egg-shell is only split so as to allow a part of the "deutovum" to emerge (Fig. 50 *D*), but in many other Acarina, *e.g.*, *Atax* and *Trombidium*, the egg-shell is quite cast off, and the embryo (or larva) continues to develop, surrounded only by the cuticular deutovum (Figs. 52 and 53, *A* and *B*). The limbs only now become jointed, the eyes appear, and the inner organisation becomes perfected (Fig. 53 *B*).

The eggs of *Atax Bonzi* are usually laid on the gills of the Lamellibranch (*Unio*) in which this Acarid lives for a portion of its life. When the embryo is sufficiently mature, it breaks through the deutovum and, as a six-limbed larva, passes into the respiratory cavity of its host. The larva of most Acarina lead a free life.

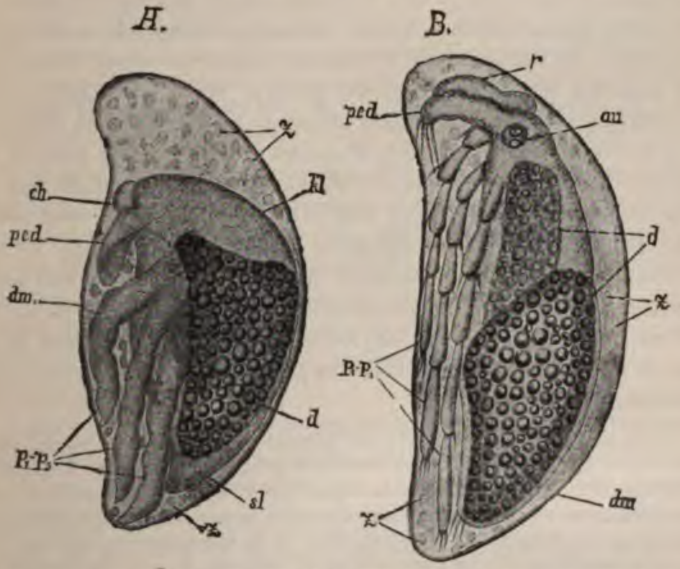

FIG. 53.—Two stages in the development of the hexapod larva of *Atax Bonzi* enclosed within the cuticular deutovum (after CLAPARÈDE). *au*, eye; *ch*, chelicerae; *d*, yolk; *dm*, cuticular deutovum; *kl*, cephalic lobe; p_1-p_3, three pairs of limbs; *ped*, pedipalps; *r*, proboscis (derived chiefly from the chelicerae); *sl*, caudal lobes; *z*, cells between the body-integument and the outer membrane ("haemamoebae").

The formation of larval integuments within the egg recalls the processes which, under similar circumstances, take place in the Crustacea. The early secretion of the cuticular envelopes, as, for instance, in *Atax*, finds its analogue in the formation of the blastodermic cuticle in many Crustacea. The sac-like envelope recurs in *Apus*, the embryo of which leaves the egg enclosed in such an envelope, and within it probably passes through part of its development until it reaches the *Nauplius* stage. There are other Crustacean larval integuments which form only at a later stage, as in some Acarina, and which are consequently already provided with appendages (*cf.* Vol. ii., p. 118).

The Larva. *The hexapod Acarid larva* shows a strong general resemblance in structure to the adult.* This is especially the case when the manner of life of the larva is the same as that of the imago, as, for example, in the *Halacaridae* (*Halacarus spinifer*, LOHMANN, No. 92). The same resemblance occurs in many *Trombidiidae*, while in other members of this family the larvae differ in structure from the adult. The larva is chiefly distinguished from the adult by the more primitive character of its organisation, especially of the segmentation of the body. In the embryo of *Tyroglyphus siro* there is, at the posterior part of the cephalo-thorax, a distinct division into three segments, which can still be found in the larva (CLAPARÈDE). These segments correspond to the pairs of limbs. In the larva of *Trombidium*, the cephalo-thorax shows six segments corresponding to the pairs of limbs (HENKING). Segmentation even appears in the abdomen in *Trombidium* (Fig. 52) and the *Oribatidae* (HENKING, MICHAEL, No. 97). This part of the body is then larger than in the *Gamasus* larva illustrated in Fig. 54. The abdominal segmentation may also be retained in some cases, like that of *Alycus roseus* described by KRAMER (No. 89). In this Acarid, the abdomen of the adult female is marked out into seven distinct segments, and segmentation can also be recognised in the thorax. Segmentation of both cephalo-thorax and abdomen seems also to take place in members of the genus *Tarsonymus* (*Dendroptus*, KRAMER, Nos. 87 and 88).

According to HALLER (No. 83) and OUDEMANS (No. 11), the Acarina possess from three to four pairs of mouth-parts, a greater number than has hitherto been assumed. Ontogenetically, however, this view is not supported, as only the rudiments of the two well-known pairs of mouth-parts (chelicerae and pedipalps) are recognisable (Figs. 51–53). It is now generally admitted that HALLER was in error in his attempt to prove that the Acarina had two pairs of maxillae like the Insecta.

The frequent appearance of a furrow between the second and third legs has led many observers to conclude that the part lying behind this furrow belongs to the abdomen, and that the two posterior pairs of legs are abdominal appendages. There is, however, considerable disagreement on this point, which further is not supported by ontogeny. HENKING in particular states that this does not hold good for *Trombidium*, nor, in his opinion, for any Acarids. These two posterior legs are attached to what is commonly called the abdomen; if the term be incorrectly applied, then it appears that the Acarina have no abdomen.

The mouth-parts of the larva already show the character of those of the adult, *i.e.*, the chelicerae,† with the basal parts of the pedipalps, unite to form a proboscis (Fig. 53 *B*). The greater part

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* [See footnote, p. 97.—ED.]

† [See footnote, p. 97.—ED.]

of each pedipalp forms a palp. The cavity of the proboscis leads into a muscular pharynx, which is followed by the cylindrical oesophagus. This latter traverses the central nervous system, which (in *Trombidium*, HENKING) consists of a large ventral ganglionic mass and a pair of smaller supra-oesophageal ganglia. The oesophagus (in *Gamasus*) passes into the spacious metenteron, from which the hepatic caeca extend anteriorly and posteriorly (Fig. 54, *ls*). The metenteron narrows again posteriorly and enters the rectal vesicle. Here the two large Malpighian vessels (*vm*), which have until now been regarded as outgrowths of the proctodaeum, take their rise.*

If the so-called *Malpighian vessels* of the Scorpiones and the Araneae should prove to be diverticula of the enteron, as may be conjectured (pp. 20 and 83), their origin would have to be more thoroughly investigated in the Acarina also. Since the proctodaeum in these latter has, as opposed to the enteron, a certain independence (HENKING, MACLEOD), the question as to the nature of these appendages would perhaps be easier to decide in the Acarina.

The anus lies at the end of the abdomen, or, as in *Trombidium*, is shifted forward. In *Trombidium* there is a constriction in the metenteron between the thorax and the abdomen, and at this point lie (in the first abdominal segment) two bean-shaped bodies which HENKING considers to be rudiments of the genital glands. These would therefore at first be paired, and only in the further course of development fuse to form the unpaired genital gland known in the adult.

Among the internal organs we have still to mention the heart, which is present in some Acarina though not in all. In *Gamasus* it lies as a rounded organ at the posterior end of the abdomen (Fig. 54, *h*). It has one pair of ostia and passes anteriorly into an aorta. It is suspended by the fibres of connective tissue or muscle-fibres from the dorsal body-wall.

The compact form of the heart is connected with the reduction undergone by the whole body in the Acarina. WINKLER, who has closely studied this question (No. 105), points out that, in the Pseudoscorpiones (young form of *Obisium silvaticum*), the heart is still somewhat long, yet is provided with only one pair of ostia (at the posterior end). The heart of the young Phalangid, in which two pairs of ostia occur, is also reduced, though to a less degree.

In the larva of *Trombidium*, between the first and second pairs of limbs, there is on each side a crescent-shaped projecting structure (Fig. 52, *ut*) produced by a thickening of the chitinous cuticle. At

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* [This description is probably correct so far as *Gamasus* is concerned, except perhaps in the question of where the metenteron ends and the proctodaeum begins, but it must not be applied to all Acarina.—ED.]

the deutovum stage, a funnel-shaped structure joins each of these thickenings externally, being attached at its narrowed end to the cuticular deutovum. An aperture is found here (Fig. 52, *st*), and this, together with the crescent-shaped structure at the surface of

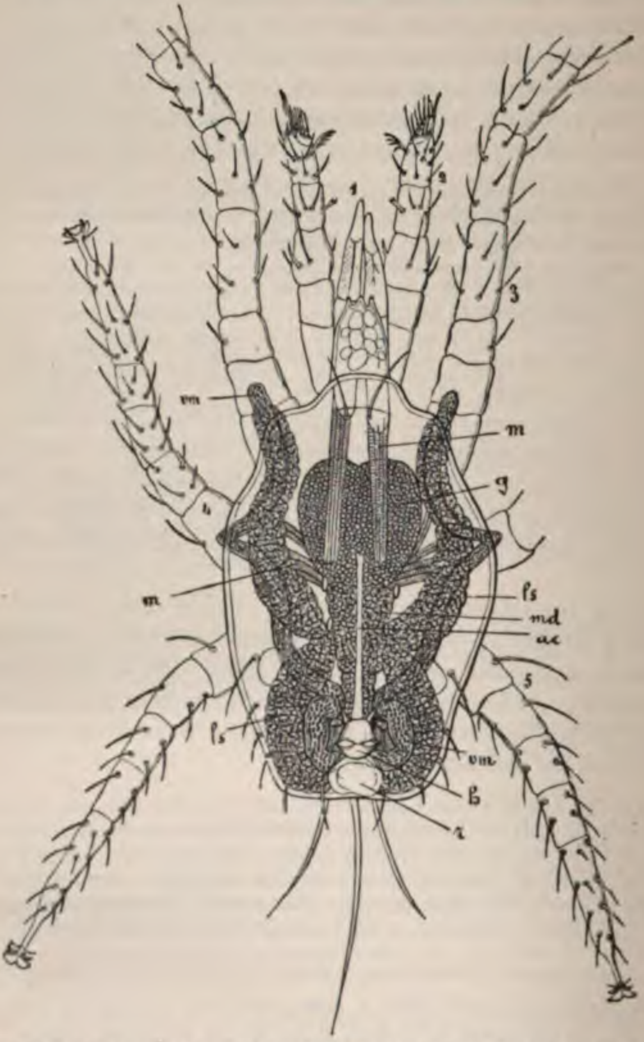

FIG. 54.—Larva of *Gamasus fucorum* (after WINKLER, from LANG's *Text-book*). *1*, chelicerae; *2*, pedipalps; *3*-*5*, ambulatory limbs; *ac*, aorta cephalica; *g*, brain; *h*, heart; *ls*, hepatic caeca; *m*, muscles (retractors of the chelicerae); *md*, metenteron; *r*, rectal vesicle; *vm*, Malpighian vessels.

the larva, HENKING is disposed to regard as a stigma.* The aperture, by means of the funnel, introduces air into the embryo. When ecdysis takes place, the funnel naturally becomes detached from the stigma (Fig. 52). Such "primitive tracheae" are found in corresponding positions in the larvae of other Acarina as well. More than half the Acarina are without eyes in all stages. Some of the free-living larvae possess one or two pair of eyes, lying at the anterior margin of the brain. Since this latter has shifted far back, the eyes also lie far back above the bases of the second pair of limbs (*Trombidium*, *Atax*, *Tetranychus*). The middle part of the cephalo-thorax has thus shifted forward beneath the anterior part.

The Nymph. After the larva has remained in the form described for a longer or shorter time, according to its manner of life, further changes take place. In *Atax Bonzi*, the larva bores into the branchial tissue of its Lamellibranch host, and loses its capacity for movement. The soft parts now become detached from the chitinous cuticle as in a typical ecdysis; the limbs draw back from their chitinous sheaths and become nearly absorbed, remaining however as small knobs. The chitinous cuticle itself swells up by the absorption of water, and the body, which has secreted a fresh cuticular covering, swims about as an almost spherical body inside the detached shell. This process resembles to a great extent that described for *Myobia* during the formation of the larva. The limbs then grow out again,† a fourth pair being added. The larva in this form is known as the nymph, and resembles the adult in its shape and also in the number of its limbs, but does not quite equal it in perfection or in sexual maturity. It commences its free life by breaking through the larval integument.

The new pair of limbs is always the fourth, at least this has been established in several forms, *e.g.*, *Trombidium* (HENKING), *Ixodes*, *Tarsonymus* (*Dendroptus* of KRAMER); in aquatic forms, according to KRAMER (No. 87), especially in the genus *Nesaea*, one of the first two pairs of limbs was newly added. LOHMANN observed that in the *Halacaridae* the second pair of limbs developed very slowly, although he also regards the fourth pair as the one newly added. OUDEMANS (No. 11), on the contrary, lays special stress on the fact that, in the larva of the *Oribatidae*, the new pair of limbs is intercalated between the second and third of those already present.‡

The transition from larva to nymph in other forms is not so simple as in the case described. The six-limbed larva of *Rhyncholophus*

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* [It is very doubtful if this be a stigma; analogy with other families would point to a different conclusion.—ED.]

† [See footnote, p. 97.—ED.]

‡ [Both KRAMER and OUDEMANS appear to be in error on these points.—ED.]

oedipodarum, which attaches itself to the body of an Oedipod, here undergoes ecdysis, and, beneath the larval integument, a sac-like pupal envelope without appendages, resembling the deutovum, develops. From this the larval integument is for the most part stripped off, but a portion remains covering the posterior third of the body as a transparent integument, in which the three larval limbs are still recognisable. A pupa is thus formed, following the six-limbed larva and giving rise to the nymph (v. FRAUENFELD, No. 79).

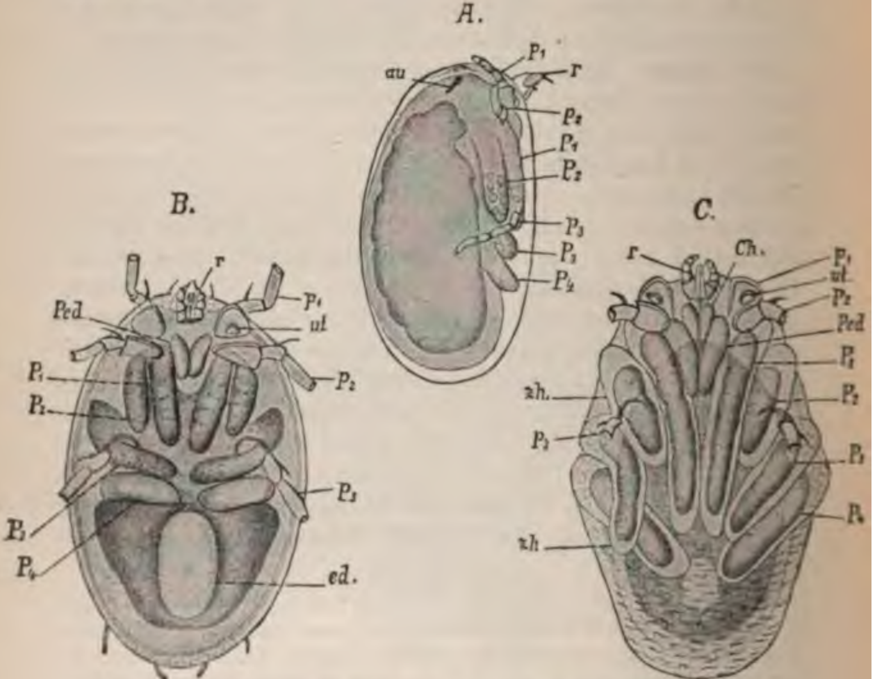

FIG. 55.—Larva of *Trombidium fuliginosum*. Formation of the pupa and nymph (after HENKING). *au*, eye; *ed*, proctodaeum p_1-p_3, larval limbs; *r*, proboscis (chelicerae and pedipalps) of the larva; *Ch*, chelicerae; *Ped*, pedipalps; P_1-P_4, limbs of the nymph; *ut*, primitive trachea; *zh*, intermediate integument.

The processes that take place in *Rhyncholophus* help us to understand the more complicated processes in *Trombidium* described by HENKING. The larva here, as in the cases already described, passes into a resting stage. After having completely filled its intestine by sucking the juices of Aphides, it creeps into earth. The body is distended, and the soft parts withdraw from the chitinous skin.

As in the pupation of Insects, histolytical processes take place, for the tissues have a more or less degenerate appearance (HENKING, No. 85; MICHAEL, No. 97). According to GUDDEN (No. 81) and MÉGNIN (No. 96), there is even complete disintegration of the tissues, whereby the resemblance to Insects is increased. Similar processes occur when the nymph changes into the imago, and no doubt have already taken place during the formation of the larva in the egg (deutovum and tritovum).

In consequence of the withdrawal of the soft parts from the larval integument, the latter appears as a mere envelope around the inner body (Fig. 55 *A*), all the more so that the empty cases of the limbs usually break off (Fig. 55 *A–C*). Within the old larval integument another cuticular integument is now formed (HENKING); this is the pupal envelope of the *Rhyncholophus*, and not the definitive chitinous integument of the nymph. This integument (the so-called intermediate integument of CLAPARÈDE, or apoderma of HENKING), in *Trombidium*, is not sac-like as in *Rhyncholophus*, but forms coverings for the limbs now found on the nymph (Fig. 55 *C*). Beneath it the chitinous cuticle of the nymph first develops. It appears that the pupa can cast off the larval integument, but does not usually do so, the mature nymph breaking through both integuments when it hatches.

The statements of HENKING as to the intermediate integument appear to us somewhat obscure. According to this writer, the intermediate integument, as well as that formed later, when the nymph changes into the imago and the corresponding "deutovum" membrane are secreted by the isolated cells, which appear beneath the old larval integument or the egg-shell (Fig. 53 *A* and *B*, *z*, CLAPARÈDE's haemamoebae). The comprehension of these processes is in this way rendered more difficult. HENKING's statements on this point are not definite, and we are inclined to imagine that the intermediate integument is separated from the subjacent hypodermis, like the larval integument above it.

The transformation of the nymph into the adult closely resembles that of the larva into the nymph. The latter buries itself and enters upon a resting pupal stage. Beneath the old nymph-integument, an intermediate integument and the new chitinous cuticle again develop (Fig. 56, *zh*). The limb-cases of the nymph, which, as before, have become empty, are partially thrown off (Fig. 56); the nymph-integument itself breaks up in some parts, and the perfect animal finally bursts through the integuments that surround it, to start life afresh as imago. It is larger than the nymph, but smaller than a sexually mature imago, though it possesses the organisation of the latter. Sexual maturity is attained by further growth and the complete development of the genital organs.

As already mentioned, histolytical processes take place during the transformation of the nymph into the imago. These do not affect all the organs, the genital organs being entirely unaffected by them. The tracheal system of the nymph, the stigma of which lies at the base of the chelicerae, does not pass over to the adult, but the tracheal tubes remain in the cast-off larval integument (HENKING). The "primitive tracheae," mentioned above, are entirely unconnected with the adult tracheal system.

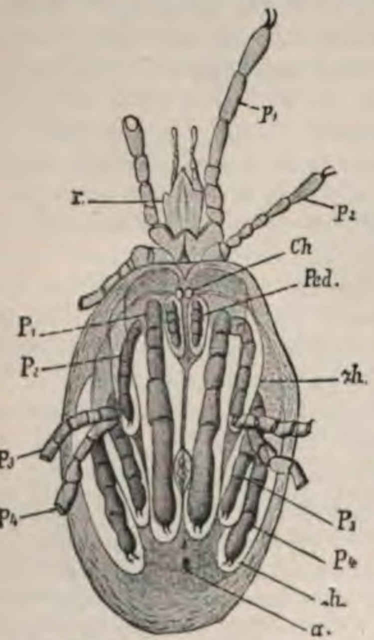

FIG. 56.—Nymph of *Trombidium fuliginosum* in the stage of the development of the pupa and imago (after HENKING). *a*, anus; *ch*, chelicerae of the imago; P_1–P_4, limbs; *Ped*, pedipalps of the imago; p_1–p_4, limbs of the nymph (partly broken off); *r*, proboscis (chelicerae and pedipalps) of the nymph; *zh*, intermediate integument.

Summary. Deviations from the usual course of development. *The development of the Acarid, from the egg to the adult, consists of a succession of larval and pupal stages.* Even within the egg a stage occurs (the deutovum) which greatly resembles the later pupal stages. This leads, after a moult, to the free larva with six limbs, which passes into a resting stage, and through it develops either directly or through the development of a pupal integument into the eight-limbed *nymph*. This also passes into a resting stage, casts off the nymph-integument, and after the formation of another pupal envelope gives rise to the young Acarid, which resembles in form the sexually mature adult.*

The above is merely a general account of the course of development in the Acarina, and is not by any means an exhaustive description, since individual families, genera, and species differ in one point or another. A really complete account would be far beyond the scope of this book, not only because of the

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* [All stages not sexually mature are considered nymphal; there are generally several nymphal ecdyses; in the *Oribatidae* two such ecdyses occur, together with a final one, in which the nymph passes into the sexually mature Acarid.—ED.]

number of statements (not indeed always reliable) made as to post-embryonic development, but also because of the number of variations occurring. We must therefore refer to the literature already quoted for further particulars, and restrict ourselves to the description of a few ontogenetic peculiarities.

The formation of the deutovum-membrane in the Acarid egg is apparently very common, and yet it seems to be indisputable that in some forms it does not take place. CLAPARÈDE, who has given special attention to this point, states that the six-limbed larvae of *Tetranychus* hatch direct out of the egg-shell, without previously being surrounded by a special chitinous envelope. The appearance of a six-limbed larva also is not universal, although it occurs in most families.* In *Phytopta*, for example, the larvae are four-limbed, *i.e.*, provided with only two pairs of limbs, and some have been disposed to regard this as a primitive condition. But since, according to NALEPA (Nos. 100 and 101), the adult *Phytopta* also has only four limbs, this must be considered as a secondary condition both in the larva and in the imago. The great preponderance of the abdomen in the *Phytopta* and the consequent length of the body must also be regarded as a specialised condition. It is interesting, in this connection, to institute a comparison with the *Demodicidae*, which also have long abdomens. The six-limbed larva is found in its development and, according to CZOKOR (No. 78), passes through a course essentially agreeing with that described above.

Taking into account the transformation of the six-limbed larva into the eight-limbed nymph, the occurrence of a four-limbed larva has been thought possibly to denote the more primitive character of the four-limbed form, from which the six-limbed form was to be derived. But we have already shown that such a conclusion is unwarrantable. Some light is thrown on the occurrence of the six-limbed larva by WINKLER's observations of *Gamasus crassipes*. Although the larva of this form has six limbs, four pairs were distinctly developed in the younger embryo (Fig. 57 *A* and *B*). WINKLER's account is so clear, that all doubt appears to be excluded.† We must assume that one pair degenerates during a moult that takes place within the egg (formation of the deutovum). Shortly before the embryo hatches, when the limbs are already provided with the characteristic setae, there are only three pairs (Fig. 57 *C*). This statement, which we are hardly justified in doubting, is a strong argument in favour of the secondary origin of the six-limbed larva.

The eight-limbed embryos of *Gamasus crassipes* observed by WINKLER appear to be in a lower developmental stage than the six-limbed embryos (Fig. 57 *A–C*). We therefore assume that, in this form, a stage like that found in *Pteroptus vespertilionis* is left out, this Acarid having an *abbreviated course of development*. The embryo of *Pteroptus* commences free life with eight limbs, *i.e.*, at the nymph stage. It could, however, be shown that the embryo passes through a six-limbed stage in the egg while the latter is still within the mother (NITZSCH).‡

Limnesia pardina also leaves the egg as a nymph (NEUMANN). The young of the *Phytopta*, when they hatch, are very like the sexually mature adult, having

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* The six-limbed larvae have been observed in the *Tetranychidae*, *Hydrachnidae*, *Halacaridae*, *Oribatidae*, *Trombidiidae*, *Gamasidae*, *Ixodidae*, *Tyroglyphidae*, *Dermaleichidae*, *Sarcoptidae*, *Demodicidae*, etc.

† [This has since been confirmed by WAGNER in *Ixodes*.—ED.]

‡ [This observation has not been confirmed, and appears very doubtful; but cases probably exist in which the whole hexapod stage is passed through in the egg.—ED.]

only two pairs of limbs, and fully-developed mouth-parts. They differ from the adult chiefly in the absence of the external genitalia. These are developed in the course of two moults, and reproduction can now take place (NALEPA, No. 100). The development of *Sphaerogyna ventricosa* appears still more abbreviated. This Acarid, the female of which is distinguished by the greatly swollen abdomen, is ovo-viviparous. The egg, after being laid, yields the sexually mature male and female, and copulation takes place soon after birth (LABOULBÈNE and MEGNIN).

The course of development may be lengthened by the occurrence of a second nymph-stage following that which proceeds from the larva, and more or less resembling it in form. This is found in *Halacarus spinifer* (LOHMANN, No. 92), and in various *Gamasidae* (KRAMER, No. 90, WINKLER, No. 106), but it ought to be more definitely ascertained whether these nymphs do not correspond to the pupal stage in other Acarina. It appears, further, that the nymph may be capable of reproduction before it attains the form of the sexually mature animal (CANESTRINI). This point was established for the *Gamasidae*. BERLESE distinguishes in this family several ontogenetic series which he describes as normal, and in which the larva, the nymph, and the imago succeed one another in the usual manner, and others which are abnormal, and in which *earlier stages, i.e., nymphs, are already capable of reproducing themselves parthenogenetically.* Such forms do not seem to attain to the complete form of the sexual animal.

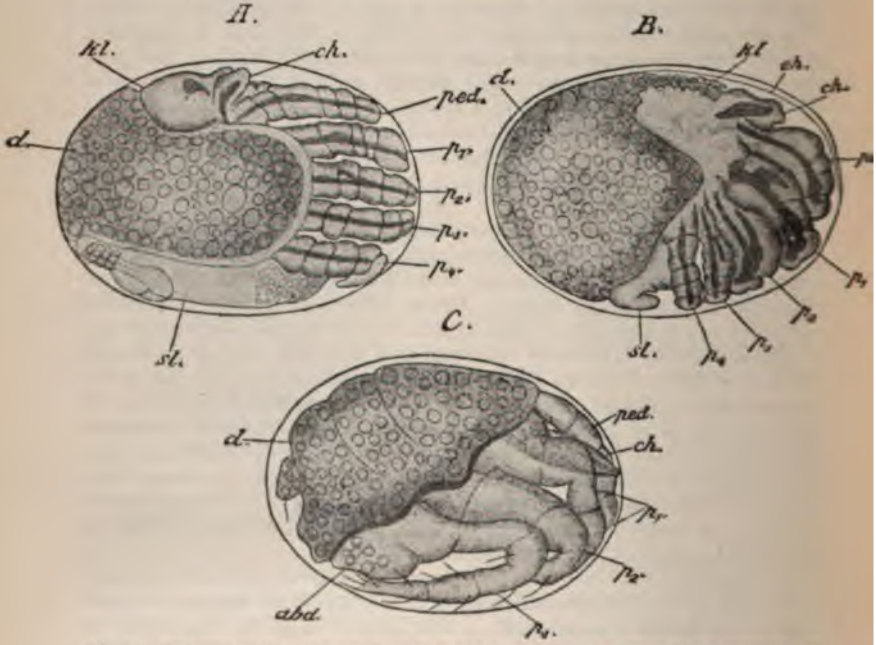

FIG. 57.—Embryos of *Gamasus crassipes* after the removal of the external egg-envelope, at various stages (after WINKLER). *abd*, abdomen; *ch*, chelicerae; *d*, yolk; *eh*, the cuticular embryonic integument; *kl*, cephalic lobe; *ped*, pedipalps; p_1-p_4, limbs; *sl*, caudal lobe.

It is said that several forms capable of reproduction may occur in this way in one and the same species; *Gamasus tardus*, for instance, has no less than five such different forms, each of which might be taken for a different species (BERLESE).* These are evidently very complicated conditions, which are far from being sufficiently understood. There is no doubt that early stages of development have repeatedly been regarded as different species, as is now definitely proved in the case of the well-known genus *Hypopus* (MEGNIN, Nos. 94 and 95, MICHAEL, Nos. 98 and 99). The members of this genus are minute creatures with a smooth chitinous shell, convex on the dorsal side and flattened on the ventral side, covering the whole of the body. Acarids with this characteristic appearance are often found on larval and on adult Insects, Myriopoda, etc., and were long regarded as adults. A closer study of the course of their development, however, proved that they merely represent early ontogenetic stages of *Tyroglyphus* and related genera, which, as a result of hitherto unknown circumstances, have deviated from the usual form of the nymph. These variations only affect isolated individuals, and it has been attempted to trace them back to unfavourable external conditions, which brought about such a modification of the inner organisation (MEGNIN). This explanation of the origin of the heteromorphic (*Hypopus*) forms has been disproved by MICHAEL.

General Considerations.

Attempts have been made to separate the Acarina from the Arachnida, and to give this group the same value as the larger divisions of the Arthropoda (Arachnida, Myriopoda, Hexapoda, HALLER, No. 83, A. C. OUDEMANS, No. 11). The grounds given for this classification appear to us too insufficient to deserve further discussion (p. 100). It rather appears to us that in the organisation and development of the Acarina there is sufficient resemblance to the Arachnida to justify their being classed among these latter, in accordance with the view until now commonly held. The Acarina represent a group of the Arachnida with highly specialised development, and are thus strongly differentiated in individual points of organisation from other Arachnids. Even the course of development has been influenced, and shows peculiarities which do not occur in other Arachnids. The chief of these are the different consecutive larval and pupal stages, and the free larval form provided with only six limbs. This latter must be considered as a secondary peculiarity. The best proof of this would be afforded by the appearance of a fourth pair of limbs in embryonic stages, which precede the six-limbed larva, if the statements made on this subject by WINKLER (No. 106, *cf.* p. 107) should be confirmed.†

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* [According to MICHAEL both these observations are erroneous.—ED.]

† [This has been done for *Ixodes* by WAGNER.—ED.]

VIII. General Considerations regarding the Arachnida.

In studying the Arachnida, the point of greatest importance and interest consists in their relationship to those divisions of the Arthropoda classed with them as Tracheata, *i.e.*, the Myriopoda and the Insecta. The Myriopoda, on account of their usually long form of body and the slight differentiation of the different parts of the body, demand less attention in this respect than the Hexapoda, in which the very marked division of the body into three regions calls for comparison with the segmentation of the Arachnida. In such a comparison, however, a serious difficulty at once arises in the different number of segments, and especially of limbs, found in the two groups.* The fusion of segments which often takes place among the Arachnida is of less consequence, since this may also occur to a greater or lesser degree among the Insecta. *The fusing of the head and the thorax to form the cephalo-thorax* must nevertheless be emphasised as an important Arachnidan character.

The Insects, as is well known, carry on the head a pair of antennae, a pair of mandibles, and two pairs of maxillae, which, on account of their structure and ontogeny, are justly regarded as limbs; further, there are three pairs of limbs on the thorax. The Arachnida have only two pairs of cephalic limbs (the chelicerae and the pedipalps), but four pairs of legs on the thorax. The attempts which have been made to harmonise these differences are too numerous to be treated here in detail. According to what may be described as the prevailing view, there is no homologue in the Arachnida for the antennae of the Insecta, but the chelicerae may be homologised with the mandibles, the pedipalps with the first maxillae, and the four ambulatory limbs with the second maxillae and the limbs that follow them. The chelicerae have, however, by some been considered to correspond to the antennae. We are not disposed to accept either of these views, but, for reasons to be given later, compare the chelicerae to the second antennae of the Crustacea, for which a homologue is wanting in the Insecta. The first antennae of the Crustacea, which correspond to the antennae of the Insecta, are not present in the Arachnida. The pedipalps can at once be homologised with the mandibles of the Insecta (and Crustacea), the four pairs of ambulatory limbs with the two pairs of maxillae and the legs of the Insecta, but in this case one pair of thoracic extremities is wanting in the Arachnida. This, however,

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* [On this whole discussion compare Editorial note, p. 117.]

does not appear to us important, since we attach no great value to this comparison of the Arachnida with the Insecta, and seek for the relationships of the former not so much in the domain of the "Tracheata" as among the branchiate forms, viz., the *Xiphosura*, as RAY LANKESTER and others have also done. We are, therefore, inclined to agree with those zoologists who consider *the Arachnida and the other air-breathing Arthropoda as two distinct series*, and also assume a *separate origin for the tracheae in these two divisions.* The agreement existing between the organisation of the Arachnida and that of the Xiphosura compels us to adopt this view.

We have already pointed out the agreement in outer structure between the Scorpiones and *Limulus* (Vol. ii., p. 357), especially in the numbers of the segments and limbs. In *Limulus*, as in the Arachnida, we find six pairs of limbs on the cephalo-thorax, so that a homology is suggested. We have just compared the first pair of limbs, the chelicerae, to the second antennae of the Crustacea, chiefly because the ganglia of these limbs, which arise post-orally, become united with the supra-oesophageal ganglion, as is the case also with the second antennae in the Crustacea (Vol ii., p. 164), and this process gains in significance when it is found repeated in the maxillary ganglia of *Peripatus* (p. 193). No such process is to be found in the Insecta, and we conclude that the limb in question is wanting in them.

We must not neglect to record the fact that, in the Opiliones and the Acarina, the chelicerae are said to be innervated from the thoracic ganglionic mass (LEYDIG, No. 40, *b*, and WINKLER, No. 106). A final elucidation of this point is very desirable.

The presence in the Araneae of another pair of cephalic limbs besides the two already mentioned has repeatedly been maintained. Two prominences are said to appear in front of the rudiments of the chelicerae and again to disappear (CRONEBERG, JAWOROWSKI). It was assumed that these conjectural limbs became united with the rostrum (CRONEBERG, LENDL*), which, according to other observers, was found to have a paired rudiment (SCHIMKEWITSCH). There was a general tendency to seek in the rostrum the rudiment of one, or, indeed, perhaps of several pairs of limbs, and it was thought that this could even be proved in the adult animal (Scorpiones, Solifugae,

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* According to LENDL, the vestigial limbs lie between the chelicerae and the pedipalps, and correspond to the mandibles of the Insecta, while the chelicerae, by their position and their manner of moving, show themselves to be true antennae. The shifting forward of the pedipalps pressed the conjectural mandibles against the rudiment of the upper lip, so as to fuse with it.

Acarina—CRONEBERG). It should be noted that, according to SCHIMKEWITSCH, the so-called lower lip also arose from a similar paired rudiment, but in this case a pair of limbs seems out of the question.

If such a vestigial pair of cephalic limbs is really present, it must be regarded (CRONEBERG, JAWOROWSKI) as the missing antennae, and would be homologous with the first antennae of the Crustacea. This would necessitate no essential modification of our view. The first antennae, which were present in the ancestors, would still occur in the Araneae as vestiges, the chelicerae, however, corresponding to the second antennae.

The pedipalps were compared by us with the mandibles of the Insecta. Each is composed of a masticatory ridge and a many-jointed palp. In the embryonic rudiment, however, both parts are said to consist of a number of joints; if so, this limb would show a very primitive character, and a certain agreement with the biramose extremities of the Crustacea (JAWOROWSKI). Indications of this biramose character are said to be found in the rudiments of other limbs also (JAWOROWSKI).

Further, whichever pair of limbs (chelicerae or pedipalps) is compared with the mandibles of the Insecta, the many-jointed character of the Arachnid limb affords a significant contrast to the Insectan mandible, which always consists of a single joint. Another primitive character is found in the presence of masticatory blades on the third and fourth limbs (in the Scorpiones and Opiliones), these extremities being thus partly utilised as mouth-parts, like the thoracic limbs of *Limulus* which surround the mouth. The presence of pincers on the anterior limbs might also well be regarded as primitive, since such pincers are found in *Limulus*. We do not, however, lay any great stress upon this, as similar structures may arise independently of each other.

The condition of the cephalo-thorax and its appendages in the various divisions of the Arachnida shows far more agreement with those of the Insecta than is found in the next section of the body—the abdomen—even if we overlook the reduced conditions which are exhibited here in the Acarina. We must here mention that the Solifugae, owing to the fact that the three posterior cephalo-thoracic segments are free, while the anterior region becomes swollen in a manner suggestive of a head, have a certain resemblance to an insect. In addition to this, the abdomen shows the same number of segments as in the Insecta, and a pair of stigmata appears on the first "thoracic" or fourth cephalo-thoracic segment. These peculiarities have led to the Solifugae, which breathe through tracheae, being brought into relation with the Insecta; but we have already shown (p. 36) that we cannot regard these characters of the Solifugae as primitive, nor consider the Solifugae themselves as intermediate forms between the Arachnida and the Insecta. In judging of the relationships of the Solifugae, it is important to note that in them also the chelicerae are innervated from the brain (WEISSENBORN, No. 16), and are thus proved to be homologous with the chelicerae of other Arachnids. An attempt to compare them with the antennae of the Insecta in order to explain their innervation will hardly be made, their whole development being opposed to this. In making a comparison with the Insecta, we should conclude rather that the antennae, which are to be regarded as a pair of cephalic limbs, are here wanting.

The *abdomen* of the Arachnida is characterised chiefly by the great reduction of its segmentation, except in some divisions however, where the segments are very distinct. In the Scorpiones, the posterior part of the body is divided into a pre-abdomen and a post-abdomen, and is of great length. It might, indeed, be considered as doubtful whether the lengthening of this part were not secondary, but for the fact that other Arachnida, during embryonic life, have sometimes this same number of segments, and also show indications of the division into pre- and post-abdomen (Araneae, pp. 50 and 57).

In the fossil Xiphosura (*Hemiaspis*, *Belinurus*), as well as in the Gigantostraca, the number of abdominal segments is larger than in *Limulus*, this makes it very probable that the abdomen of the latter has arisen through the fusion of a number of post-abdominal segments, and is thus homologous with the post-abdomen of the Scorpiones (Vol. ii., p. 358). The latter thus show, in the retention of the richly-segmented abdomen and in their segmentation generally, a very primitive character. It has been conjectured that the length and mobility of the abdomen are connected with the poison-sting which arms its extremity, and which is thus the more easily brought into use (WEISSENBORN).

Great concentration of the organs is evident in the Arachnida, and the further forms are removed from those which we may rightly consider as the most primitive, the greater is the degeneration found in them, this degeneration reaching its highest degree in the Acarina. The derived forms of the Arachnida are thus simpler in their organisation than the primitive forms, especially as certain systems of organs (circulatory and respiratory systems) may partly, or wholly, degenerate.

The *abdominal limb-rudiments* are of peculiar importance in the comparison of the Arachnida with other Arthropods. Their number in the Scorpiones, as in *Limulus*, is six. [? *cf.* Brauer, Kishinouye.] It is possible that in the Araneae, also, the same number of abdominal appendages was originally present (p. 51). The Arachnida, like the Insecta, were derived from forms provided with a larger number of limbs. The first pair [second, pp. 10, 25, 57], is related to the genital aperture, while the following pairs show on their posterior surface the invaginations which give rise to the lungs. The lungs of the Arachnida may therefore be homologised with some probability with the gills of the Xiphosura (Vol. ii., p. 358, and Vol. iii., p. 77). This implies an origin for the Arachnidan tubular tracheae different from that in other "Tracheata" (*Peripatus*, Myriopoda, Insecta), for there can be no doubt that the tracheae in the Arachnida are in the closest connection with the lungs.[*] Although the tracheae in a few Arachnids, *e.g.*, the Solifugae, the Opiliones, and some Pseudoscorpiones and Acarina, seem to resemble each other greatly in structure, they must, in the one case, be derived from lungs or gills, and, in the other cases, from simple integumental depressions. Their later similarity of structure must be regarded as a phenomenon of convergence.[†]

The presence of the stigmata in the abdomen only is in accordance with the view of the origin of the respiratory organs here adopted, but an exception occurs in the first pair of stigmata of the Solifugae which lies on the first "thoracic," or, rather, fourth cephalo-thoracic, segment. This must for the present be regarded as a secondary acquisition, and we may similarly try to explain the fact that, in the Acarina, stigmata occur in the cephalo-thorax at various points, often very far forward, in the cheliceral region. Similar displacements of the stigmata are also known to occur in *Scolopendrella*, where they also appear in the head in an unusual manner.

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[*] [See Simmons and Purcell (App. to Lit. on Araneae, Nos. VII., VIII.) and footnotes, p. 78.—Ed.]

[†] [Tubular tracheae are not restricted to these four groups, but are also found in many Araneae associated with the lungs; only the Scorpiones and the Pedipalpi have lungs alone. This has led Bernard (App. to Lit. on Arachnida in gen., No. III.) and Jaworowski (App. to Lit. on Araneae, No. II.) to the conclusion that the lung-books are not primitive structures giving rise to the trachea, but rather that both the lung-books and trachea are to be derived from simple sac-tracheae.—Ed.]

There are various other points of organisation in which the Arachnida are removed from the Insecta, but approach the Xiphosura, and perhaps even the Crustacea.

In dealing with the eyes, we tried to show that they cannot be classed together with those of the Insecta and the Myriopoda, but have had a different course of development (p. 68). They may, however, well be homologised with the median and lateral eyes of *Limulus*. In the origin of the Arachnid eyes, inversion plays an important part. Inversion has recently, also, been introduced by CLAUS as an explanation of the origin of the median eye of the Crustacea (No. 57), and it appears not impossible that a closer connection may be found later between these processes.

Further agreement between the Arachnida and the Xiphosura is found in the presence of an endoskeleton, which in the Scorpiones and *Limulus* is very similar in structure.* Another point which appears to us to be very characteristic, and which also fully applies to the Solifugae, in spite of their apparent deviation from the other Arachnids, is the presence of a large digestive gland (liver), such as does not occur in the Insecta, but is found in *Limulus* and the Crustacea. Another still more important point of agreement is yielded by the enteron and its appendages, if we grant that the testimony of ontogeny is reliable, viz., the origin of the so-called *Malpighian vessels* out of the entoderm. If this is the case, it would form an important reason for separating the Arachnida from the Insecta. Tubular appendages occur in the Crustacea at the posterior end of the metenteron; the Malpighian vessels of the Myriopoda and the Insecta are, however, of ectodermal origin.

Another point of resemblance between *Limulus* and the Arachnida is afforded by the presence of an artery running, in the Scorpiones, above the chain of ganglia, and forming a backward continuation of the oesophageal vascular ring (supra-neural vessel, supra-spinal artery); a condition similar to this is met with in the ontogeny of *Limulus*. A sub-neural artery, indeed, occurs in the Crustacea, and a supra-neural vessel is also found in the Myriopoda (a fact

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* [There is considerable disagreement regarding the homology of the endosternite. BERNARD (App. to Lit. on Scorpiones, No. I.), who has made a comparative study of the Arachnidan endosternite, comes to the conclusion that the endosternite of *Limulus* cannot be homologous with that of the Arachnids, the latter being part of an epidermal endophragmal system, while that of Limulus is mesodermal. On the other hand, SCHIMKEWITSCH (App. to Lit. on Scorpiones, No. VI.) maintains that the structure generally termed the endosternite in the Arachnida and *Limulus* is always mesodermal, and co-exists with, but is independent of, the series of ectodermal apodemes which are so conspicuous in *Galeodes*.—ED.]

which makes this point of resemblance appear of less importance), so that this feature may perhaps be inherited from a common ancestral form. A less important agreement with the genital glands of *Limulus* is afforded by the corresponding tubular network of genital glands in the Scorpiones.

The *coxal glands* of the Arachnida, derived from the mesoderm, may, according to our present knowledge, be assumed with considerable certainty to be *nephridia*, and are comparable with the organs which, in *Limulus*, occupy a corresponding position. These glands cannot be fully homologised with the antennal and shell-glands of the Crustacea, since these latter differ somewhat from them in position, *i.e.*, belong to other segments. The nephridia that were present in every segment in the ancestral form have undergone great reduction, and the remnants are retained by their descendants in different segments, a feature probably connected with the varying form of the adult body in the different groups. We need hardly point out that the possession of coxal glands (especially strongly developed in youth) is a further distinction between the Arachnida and the Insecta, the latter not possessing any glands which in their development and position could be compared with the nephridia of the ancestral form.

The Arachnid coxal glands arise from the mesoderm, the condition of which during embryonic development is a point of special importance. While, in the Insecta, the primitive segments are early subjected to change, in the Arachnida, they grow forward dorsally, and only undergo disintegration at a time when the dorsal heart is formed from them. The coelom, which disappears very early in the Insecta, is long retained in the Arachnida. This, which in itself is a primitive condition, further determines a greater simplicity in the rudiment of the heart, perhaps also in that of the coxal glands (nephridia), and probably also of the genital glands. The conditions thus produced recall those in the Annelida more than those in the remaining Arthropoda.

It appears open to question whether much stress should be laid on the agreement existing between the cleavage, and the formation of the germinal layers and of the first rudiments of the organs in the Arachnida and the processes described for the Crustacea, or whether these should be explained by a certain similarity prevailing in these processes throughout the Arthropoda. This has already been pointed out in individual cases. It must remain equally doubtful whether the youngest stage of the germ-band in the Scorpiones, which has been compared with a certain ontogenetic stage in the Trilobites (p. 6), is of special importance in this connection. It can hardly be doubted, from all that has been stated above, that there is a close relationship between the Arachnida and *Limulus*, and, consequently, points of agreement with the Trilobites might be expected. It is, in this connection, a striking fact that the Scorpiones are of such great age, and that the forms now extant are not very unlike those found in the Silurian strata (*Palaeophonus nuncius*, No. 15).

In conclusion, we must again emphasise the fact that the apparent agreement of the Arachnida with the other Tracheata must be regarded as nothing more than a similarity determined by their common Arthropodan nature and by a like development as the result of a similar manner of life. We must not assume a nearer connection between these divisions of the Arthropodan stock. We believe, rather, that the Arachnida, together with the Palaeostraca, proceeded from a common ancestral form, and subsequently diverged from one another, while the other Tracheata belong to a distinct stock, the two, however, being connected very far back.

The Arachnida, according to our view of them, form a very uniform group. The most primitive forms are those in which the body is distinctly segmented, *i.e.*, the Scorpiones and the Pedipalpi.* The Opiliones and the Pseudoscorpiones are affected by a reduction which goes still further in the Araneae, and reaches its highest degree in the Acarina, in which this far-reaching adaptation is accompanied by essential modifications in development.† Such modifications are also found in the Pseudoscorpiones, probably as the result of similar causes.

[In addition to the editorial footnotes inserted here and there referring to BERNARD's Arachnidan work, it is necessary to call separate attention to it in some detail, inasmuch as it has a profound bearing upon the question as to whether the Arachnids could be deduced from a Limuloid ancestral form. Arguing that the only scientific method of arriving at the ancestral form of the Arachnida is to compare all the known forms, and to sift out what are obviously the more primitive structural adaptations from the more specialised, this author arrives at the conclusion that the Solifugae come nearest the ancestral form in their segmentation, and in the simplicity of their endosternites. This endosternite has no resemblance whatever to the endosternite of *Limulus*, to which he would assign an entirely different origin (App. to Lit. on Arachnida in gen., No. I., and App. to Lit. on Scorpiones, Nos. I., VI.). He endeavours to show that the typical form of the Arachnidan body is an adaptation to the special manner of feeding. The Arachnids suck the blood of their victims, and, by a force-pump action of the oesophagus, distend the alimentary canal in a manner which would seriously interfere with the rest of the organisation. Their whole inner anatomy, he believes, can be shown to be simply so many adaptations to this serious

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* [According to BERNARD, the Solifugae are in this respect the most primitive.—ED.]

† [This statement is a little misleading, for, in the adult Opiliones, only six segments are visible in the abdomen, while, in the Pseudoscorpiones, there are ten to eleven; further, although the abdominal somites are fused in most adult Araneae (not in *Liphistius*), yet, in the young, eight to nine segments can be recognised; these are not lost, but fused together, and, even in the Acarina, one form (Ixodes) exhibits marked segmentation (WAGNER).—ED.]

distention of the intestinal tract—adaptation, that is, of some much less specialised type than *Limulus*. All the chief organs are dealt with in detail, and, whether the author's conclusions are all of them ultimately confirmed or not, he has succeeded in placing on a new level, not only the controversy regarding the Arachnidan origin, but also (by his association of physiology with morphology) the science of the whole group. So far his views have not met with much acceptance, and the Scorpiones are still generally regarded as the most primitive Arachnids finding their nearest allies in the Merostomata.—Ed.]

LITERATURE.

Arachnida in General.

1. Croneberg, A. Ueber die Mundtheile der Arachniden. *Archiv. f. Naturgesch.* Jahrg. xlvi. 1880.
2. Eisig, H. Die Capitelliden des Golfs von Neapel. *Monographie der Fauna und Flora von Neapel. Berlin,* 1887. (On the coxal and spinning glands of the Arachnida.)
3. Fernald, H. T. The Relationships of Arthropods. *Studies Biol. Lab. Johns Hopkins University. Baltimore.* Vol. iv. 1890.

4a. Grenacher, H. Untersuchungen über das Sehorgan der Arthropoden. *Göttingen,* 1879.

4b. Haase, E. Beiträge zur Kenntniss der fossilen Arachniden. *Zeitschr. Deutsch. Geologisch. Gesellsch.* Jahrg. 1890.

5. Jaworowski, A. Ueber die Extremitäten bei den Embryonen der Arachnoiden und Insecten. *Zool. Anz.* Bd. xiv. 1891.
6. Lankester, E. Ray. Limulus an Arachnid. *Quart. Journ. Micro. Sci.* Vol. xxi. 1881.
7. Lankester, E. Ray. On the sceleto-trophic tissues and the coxal glands of Limulus, Scorpio, and Mygale. *Quart. Journ. Micro. Sci.* Vol. xxiv. 1884.
8. Leuckart, R. Ueber den Bau und die Bedeutung der sog. Lungen bei den Arachniden. *Zeitschr. f. Wiss. Zool.* Bd. i. 1849.
9. Loman, J. C. C. Altes und Neues über das Nephridium (die Coxaldrüse) der Arachniden. *Bijdragen tot de Dierkunde.* Aflev. xiv. *Amsterdam,* 1887.
10. MacLeod, J. Recherches sur la structure et la signification de l'appareil respiratoire des Arachnides. *Archiv. Biol.* Tom. v. 1884.
11. Oudemans, A. C. Die gegenseitige Verwandtschaft, Abstammung und Classification der sog. Arthropoden. *Tijdschrift der Nederlandsche Dierkundige Vereenigung.* (2). Deel i. 1885–87.

12a. Saint-Remy, G. Contribution à l'étude du cerveau chez les Arthropodes trachéates. *Archiv. Zool. Exper.* (2). Tom. v. Suppl. 1887–90.

12b. Schimkewitsch, W. Les Arachnoides et leurs affinités. *Archiv. Slav. Biol.* Tom. i. *Paris*, 1886.

13. Scudder, S. H. Bearbeitung der Arachniden. Zittel's *Handbuch der Palaeontologie. München* and *Leipzig*, 1885.

14. Sturany, R. Die Coxaldrüsen der Arachnoiden. *Arb. Zool. Institut Univ. Wien.* Bd. ix. 2. 1891.

15. Thorell, T., and Lindström, G. On a Silurian Scorpion from Gotland. *K. Svenska Vetenskaps Akad. Handlingar.* Bd. xxi. 1885. *Ann. Mag. Nat. History* (5). Vol. xv. 1885.

16. Weissenborn, B. Beiträge zur Phylogenie der Arachniden. *Jen. Zeitschr. f. Naturw.* Bd. xx. 1885.

APPENDIX TO LITERATURE ON ARACHNIDA IN GENERAL.

I. Bernard, H. M. Comparative Morphology of the Galeodidae. *Trans. Linn. Soc.* 1896.

II. Bernard, H. M. The Apodidae. *London*, 1892.

III. Bernard, H. M. An endeavour to show that the tracheae of the Arthropoda arose from setiparous sacs. *Zool. Jahrb.*, Bd. v., and *Ann. Mag. Nat. Hist.* (6). Vol. xi. 1893.

IV. Gaubert, P. Recherches sur les organes des senses et sur les systèmes tégumentaire, glandulaire et musculaire des appendices des Arachnides. *Ann. Sci. Nat.* (7). Tom. xiii.

V. Hansen, H. J. Orders and characters in different orders of Arachnids. *Ent. Meddel. Kjöbenhavn.* Bd. iv.

VI. Jaworowski, A. Homologie der Gliedmassen bei Arachniden und Insekten. *Kosmos. Lemberg*, 1891.

VII. Pocock, R. I. On some points in the Morphology of the Arachnida (S. S.), with notes on the Classification of the Group. *Ann. Mag. Nat. Hist.* (6). Vol. xi. 1893.

VIII. Wagner, J. Beiträge zur Phylogenie der Arachniden. *Jen. Zeitschr. f. Naturw.* Bd. xxix. 1895.

IX. Are the Arthropoda a natural group? By ten authors. *Nat. Sci.* Vol. x.

I. Scorpiones.

17. Blochmann, F. Ueber directe Kerntheilung in der Embryonalhülle der Skorpione. *Morph. Jahrb.* Bd. x. 1885.

18. **Ganin**, M. S. On the Development of the Scorpion. (Russian, without illustrations.) *Supplement to the Protocol Univer. Kharkov.* 1867.

19. **Kowalevsky**, A., and **Schulgin**, M. Zur Entwicklungsgeschichte des Skorpions (Androctonus ornatus). *Biol. Centralbl.* Bd. vi. 1886–87.

20. **Lankester**, E. **Ray**, and **Bourne**, A. G. The minute structure of the lateral and central eyes of Scorpio and Limulus. *Quart. Journ. Micro. Sci.* Vol. xxiii. 1883.

21. **Lankester**, E. **Ray**. On the coxal glands of Scorpio, etc., and the brick-red glands of Limulus. *Proc. Roy. Soc. London.* Vol. xxxiv. 1882–83. p. 95.

22. **Lankester**, E. **Ray**. New hypothesis as to the relationship of the lung-book of Scorpio to the gill-book of Limulus. *Quart. Journ. Micro. Sci.* Vol. xxv. 1885.

23. **Laurie**, M. The Embryology of a Scorpion (Euscorpius italicus). *Quart. Journ. Micro. Sci.* Vol. xxxi. 1890.

24. **Metschnikoff**, E. Embryologie des Scorpions. *Zeitschr. f. Wiss. Zool.* Bd. xxi. 1871.

25. **Müller**, **Joh**. Beiträge zur Anatomie des Scorpions. *Meckel's Archiv. f. Anat. u. Phys.* 1828.

26. **Parker**, G. H. The eyes in Scorpions. *Bull. Mus. Comp. Zool. Harvard College.* Vol. xiii. 1887.

27. **Patten**, W. On the origin of Vertebrates from Arachnids. *Quart. Journ. Micro. Sci.* Vol. xxxi. 1890.

28. **Rathke**, H. Zur Morphologie. *Reisebemerkungen aus Taurien. Riga* and *Leipzig*, 1837.

APPENDIX TO LITERATURE ON SCORPIONES.

I. **Bernard**, H. M. The Endosternite of Scorpio compared with that of other Arachnids. *Ann. Mag. Nat. Hist.* (6). Vol. xiii. 1894.

II. **Brauer**, A. Beiträge zur Kenntniss der Entwicklungsgeschichte des Skorpions. *Zeitschr. f. Wiss. Zool.* Bd. lvii. and lix.

III. **Laurie**, M. On the development of Scorpio fulvipes. *Quart. Journ. Micro. Sci.* Vol. xxxii. 1891

IV. **Laurie**, M. On the development of the Lung-books of Scorpio fulvipes. *Zool. Anz.* 1892.

V. **Marchal**, P. La glande coxale du Scorpion et ses rapports morphologiques avec les organes excréteures des Crustacés. *Compt. rend.* Tom. cxv. (Translated in *Ann. Nat. Hist.* (6). Vol. x.)

VI. Schimkewitsch, W. Ueber Bau und Entwicklung des Endosternites der Arachniden. *Zool. Jahrb.* (*Anat.*). Bd. viii. 1894.

II. Pedipalpi.

29. Bruce, A. T. Observations on the Nervous System of Insects and Spiders, and some preliminary observations on Phrynus. *Johns Hopkins University Circulars. Baltimore.* Vol. vi. 1886–87. No. 54, p. 47.

30. Grassi, B. Intorno ad un nuovo Aracnide Artrogastro etc. I. Progenitori dei Miriapodi e degli Insetti. Memoria V. *Bull. Società Entomol. Ital.* Anno xviii. *Firenze*, 1886.

31. Tarnani, J. Die Genitalorgane der Telyphonus. *Biol. Centralbl.* Bd. ix. 1889–90.

APPENDIX TO LITERATURE ON PEDIPALPI.

I. Laurie, M. On the Morphology of the Pedipalpi. *Journ. Linn. Soc.* Vol. xxv. 1894.

II. Pereyaslawzewa, S. (1) Les premiers stades du développement des Pedipalpi. (2) Les derniers stades du développement des Pedipalpi. *Compt. rend.* Tom. cxxv. 1897.

III. Strubell, A. Zur Entwicklungsgeschichte der Pedipalpen. *Zool. Anz.* xv. (Translated in *Ann. Nat. Hist.* (6). Vol. x. 1892.)

III. Palpigrada.

31a. Hansen, H. J., and Sörensen, W. The order Palpigrada Thor. and its relationship to the other Arachnida. *Entomologisk Tidskrift.* Aug. 18th, 1897. And Grassi, No. 30.

IV. Pseudoscorpiones.

32. Barrois, J. Sur le développement des Chelifers. *Compt. rend. Acad. Sci. Paris.* Tom. xcix. 1884. p. 1082.

33. Croneberg, A. Beitrag zur Kenntniss des Baues der Pseudoscorpione. *Bull. Soc. imp. Nat. de Moscou.* Tom. ii. 1888.

34. Metschnikoff, E. Entwicklungsgeschichte des Chelifer. *Zeitschr. f. Wiss. Zool.* Bd. xxi. 1871.

35. Stecker, A. The development of the ova of Chthonius in the body of the mother, and the formation of the blastoderm. *Ann. Mag. Nat. Hist.* (4). Vol. xviii. 1876. p. 197. (Translated from *Sitzungsber. böhm. Gesellsch. Wiss. Prag*, 1876.)

APPENDIX TO LITERATURE ON PSEUDOSCORPIONES.

I. Barrois, J. Mémoire sur le développement de Chelifer. *Rev. Suisse Zool.* 1896.

II. Bernard, H. M. Notes on the Chernetidae, with special reference to the vestigial stigmata, and to a new form of Trachea. *Journ. Linn. Soc. Zool.* Vol. xxiv.

III. Bertkau, Ph. Zur Entwicklungsgeschichte der Pseudoscorpione. *C. B. Ver. Rheinl.* 1891.

IV. Bouvier, E. L. Sur la ponte et le développement d'un Pseudoscorpionide, le Garypus saxicola. *Bull. Soc. ent. France.* 1896.

V. Vejdowsky, J. F. Sur la question de la ségmentation de l'oeuf et la formation du blastoderme des Pseudoscorpiones. *Congr. internat. Zool.* ii. 1892.

V. Opiliones.

36. Balbiani, E. G. Mémoire sur le développement des Phalangides. *Ann. Sci. Nat.* (5) *Zool.* Tom. xvi. 1872.

37. Faussek, V. Ueber die embryonale Entwicklung der Geschlechtsorgane bei der Afterspinne (Phalangium). *Biol. Centralbl.* Bd. viii. 1888–89.

38. Faussek, V. Zur Embryologie von Phalangium. *Zool. Anz.* Jahrg. xiv. 1891.

39. Faussek, V. On some ontogenetic stages of the Opiliones. *Trud. ross. estestv. Obshchetsvo. St. Petersburg. Zool.* Tom. xx., pp. 46–53.

40a. Henking, A. Untersuchungen über die Entwicklung der Phalangiden. *Zeitschr. f. Wiss. Zool.* Bd. xlv. 1887.

40b. Leydig, F. Ueber das Nervensystem der Afterspinnen (Phalangium). *Archiv. f. Anat. u. Phys.* 1862.

41. MacLeod, J. Sur l'existence d'une glande coxale chez les Phalangides. *Bull. Acad. Roy. Sci. Belgique.* (3). Tom. viii. 1884.

APPENDIX TO LITERATURE ON OPILIONES.

I. Bertkau, P. Die Entwicklung der Coxaldrüse bei Phalangium. *Zool. Anz.* Bd. xv. 1892.

II. Faussek, V. Zur Embryologie von Phalangium. *Zool. Anz.* Bd. xiv.

III. Faussek, V. Zur Anatomie und Embryologie der Phalangiden. *Biol. Centralblatt.* Bd. xii. (Translated in *Ann. Mag. Nat. Hist.* (6). Vol. ix. 1892.)

IV. Faussek, V. On the ontogeny and anatomy of the Phalangidae (Russian). *Trud. ross. Obshchestvo estestv. St. Petersburg Zool.* Tom. xxii. (No. III. is a résumé of this larger work).

V. **Lebbedinsky, J.** Die Entwicklung der Coxal-drüse bei Phalangium. *Zool. Anz.* Bd. xv. 1892.

VI. **Purcell, F.** Über den Bau der Phalangidenaugen. *Zeitschr. f. Wiss. Zool.* Bd. lv. (1). 1894.

VI. Solifugae.

42. **Birula, A.** Einiges über den Mitteldarm der Galeodiden. *Biol. Centralbl.* Bd. xi. 1891–92.

43. **Cronebergg, A.** Ueber ein Entwicklungsstadium von Galeodes. *Zool. Anz.* Jahrg. x. 1887.

44. **MacLeod, J.** Sur la présence d'une glande coxale chez les Galéodes. *Bull. Acad. Roy. des Sci. Belgique* (3). Tom. viii. 1884.

45. **Lankester, E. Ray.** Limulus an Arachnid. *Quart. Journ. Micro. Sci.* Vol. xxi. 1881. p. 644.

APPENDIX TO LITERATURE ON SOLIFUGA.

I. **Bernard, H. M.** Comparative Morphology of the Galeodidae. *Trans. Linn. Soc. Zool.* 1896.

II. **Birula, A.** Beiträge zur Kenntniss der Anatomischen Baues Geschlechtorgane bei dem Galeodiden. *Biol. Centralbl.* Bd. xii. 1892.

VII. Araneae.

46. **Balbiani, E. G.** Mémoire sur le développement des Aranéides. *Ann. Sci. Nat. Zool.* (5). Tom. xviii. 1873.

47. **Balfour, F. M.** Notes on the development of the Araneina. *Quart. Journ. Micro. Sci.* Vol. xx. 1880.

48. **Barrois, J.** Recherches sur le développement des Araignées. *Journ. Anat. et Phys. Paris*, 1877.

49. **Bertkau, Ph.** Ueber die Respirationsorgane der Araneen. *Archiv. f. Naturgesch.* Jahrg. xxxviii. 1872.

50. **Bertkau, Ph.** Ueber den bau der Augen etc. bei den Spinnen. *Verhandl. Naturhist. Ver. Rheinlande und Westfalen.* Jahrg. xlii. 1885. p. 218.

51. **Bertkau, Ph.** Ueber den Verdauungsapparat der Spinnen. *Archiv. f. mikr. Anat.* Bd. xxiv. 1885.

52. **Bertkau, Ph.** Beiträge zur Kenntniss der Sinnesorgane der Spinnen. I. Die Augen. *Archiv. f. mikr. Anat.* Bd. xxvii. 1886.

53. **Bruce, A. T.** Observations on the Embryology of Spiders. *Amer. Nat.* Vol. xx. 1886.

54. Bruce, A. T. Observations on the Embryology of Insects and Arachnids. *Baltimore,* 1887.

55. Carrière, J. von. Kritische Besprechung der neueren Arbeiten über Bau und Entwicklung des Auges der zehnfüssigen Crustaceen und Arachnoiden. *Biol. Centralbl.* Bd. ix. 1889-90.

56. Claparède, E. Recherches sur l'évolution des Araignées. *Naturkundige Verhandl. Provinciaal Utrechtsch Genootshap Kunst. Wiss.* Deel i. Stuk i. *Utrecht,* 1862.

57 Claus, C. Ueber den feineren Bau des Medianauges der Crustaceen. *Anz. d. Akad. Wiss. Wien.* No. xii. 1891.

58. Emerton, H. Observations on the development of Pholcus. *Proc. Boston Soc. Nat. Hist.* Vol. xiv. 1870-71.

59. Herold, M. Untersuchungen über die Bildungsgeschichte der wirbellosen Thiere im Eie. I. Theil. Von der Erzeugung der Spinnen. *Marburg,* 1824.

60. Kennel, J. von. Die Ableitung der sog. einfachen Augen der Arthropoden, nämlich der Stemmata der Insectenlarven, Spinnen, Scorpioniden etc. von den Augen der Anneliden. *Sitzungsber. Naturf. Gesellsch. Dorpat.* Bd. viii. 1888.

61. Kingsley, J. S. The Embryology of Spiders. Critical notice of No. 72, Schimkewitsch. *Amer. Nat.* Vol. xxi. 1887.

62. Kishinouye, K. On the development of Araneina. *Journ. Coll. Sci. Imp. University, Tokio. Japan.* Vol. iv., Part i. 1891. (This journal was only accessible after this work had gone to press. The chief results recorded have, however, been referred to by us.)

63. Lendl, A. Ueber die morphologische Bedeutung der Gliedmaassen bei den Spinnen. *Mathem. naturw. Berichte aus Ungarn. Budapest* and *Berlin.* Bd. iv. 1886.

64. Locy, W. A. Observations on the development of Agalena naevia. *Bull. Mus. Comp. Zool. Harvard College.* Vol. xii. 1886.

65. Loman, J. C. Ueber die morpholog. Bedeutung der sog. Malpighi'schen Gefässe der echten Spinnen. Tijdschrift der Nederlandsche Dierkundige Vereenigung. Ser. 2., Deel i. 1885-87.

66. Ludwig, H. Ueber die Bildung des Blastoderms bei den Spinnen. *Zeitschr. f. Wiss. Zool.* Bd. xxvi. 1876.

67. Mark, E. L. Simple eyes in Arthropods. *Bull. Mus. Comp. Zool. Harvard Coll.* Vol. xiii. 1887.

68. Morin, J. Zur Entwicklungsgesch. der Spinnen. *Biol. Centralbl.* Bd. vi. 1886–87.

69. Morin, J. On the Development of the Araneae. *Zapisk. novoross. Obsh. estestv. Odessa.* Tom. xiii. 1888 (Russian).

70. Sabatier, A. Formation du blastoderme chez les Aranéides. *Compt. rend. Acad. Sci. Paris.* Tom. xcii. 1881. (*Ann. Mag. Nat. Hist.* (5). Vol. vii. 1881.)

71. Salensky, W. On the Development of the Araneae. *Zapisk. Kievsk. Obshch. estestv.* Tom. ii., Pt. i. 1871. (Russian. Abstracted in Hofmann's and Schwalbe's *Jahresb. Anat. Phys.* Bd. ii. 1875. p. 323.)

72. Schimkewitsch, W. Étude sur le développement des Araignées. *Archiv. Biol.* Tom. vi. 1887.

73. Watase, S. On the Morphology of Compound Eyes of Arthropods. *Studies Biol. Lab. Johns Hopkins University. Baltimore.* Vol. iv. 1890.

APPENDIX TO LITERATURE ON ARANEAE.

I. Damin, N. Ueber Parthenogenesis bei Spinnen. *Verh. Ges. Wien.* xliii. (Translated *Ann. Mag. Nat. Hist.* 1894.)

II. Jaworowski, A. Die Entwicklung der sogenannten Lungen bei der Arachnoiden und speciell bei Trochosa singoriensis, nebst Anhang über die Crustaceenkiemen. *Zeitschr. f. Wiss. Zool.* Bd. lviii.

III. Jaworowski, A. Ueber die Extremitäaten, deren Drüsen und Kopfsegmentierung bei Trochosa singoriensis. *Zool. Anz.* Bd. xv. 1892.

IV. Jaworowski, A. Die Entwicklung der Geschlechtsdrüsen bei Trochosa singoriensis. *Verh. Ges. deutsch. Naturf.* 1895.

V. Jaworowski, A. Die Entwicklung des Spinnenapparates bei Trochosa singoriensis, mit Berücksichtigung der Abdominalanhänge und der Flügel bei der Insekten. *Jen. Zeitschr. f. Naturw.* Bd. xxx. 1896.

VI. Kishinouye, K. Note on the Coelomic cavity of Spiders. *Journ. Sci. Coll. Japan.* Vol. vi. 1894.

VII. Purcell, F. Note on the Development of the Lungs, Entapophyses, Tracheae, and genital ducts in Spiders. *Zool. Anz.* Bd. xviii.

VIII. Simmons, O. L. Development of the Lungs of Spiders. *Amer. Journ. Sci.* (3). Vol. xlviii. Also in Tuft's Coll. Stud. No. 2.

VIII. Acarina.

The literature on the ontogeny of the Acarina is so extensive that only a limited number of the works can here be quoted. Fuller references to literature will be found in the works of Fürstenberg (No. 80), Henking (No. 85), and Lohmann (No. 92).

74. Beneden, P. J. van. Recherches sur l'histoire naturelle et le développement de l'Atax ypsilophora. *Mém. Acad. Roy. Belgique.* Tom. xxiv. 1850.

75. Berlese, M. A. Polymorphisme et Parthénogénèse de quelques Acariens (Gamasides) *Archiv. Ital. Biol.* Tom. ii. *Turin,* 1882.

76. Canestrini, G. Osservazioni intorno al genere Gamasus. *Atti del Real. Instituto Veneto d. Sc., Lett. etc.* (5). Tom. vii. 1880–81.

77. Claparède, E. Studien an Acariden. *Zeitschr. f. Wiss. Zool.* Bd. xviii. 1868.

78. Czokor, J. Ueber Haarsackmilben und eine neue Varietät derselben bei Schweinen. *Verh. k. k. zool. bot. Gesellsch. Wien.* Bd. xxix. 1880.

79. Frauenfeld, G. von. Zool. Miscellen. Rhyncholophus oedipodarum. *Verh. k. k. zool. bot. Gesellsch. Wien.* Bd. xviii. 1868.

80. Fürstenberg, M. H. F. Die Krätzmilben des Menschen u. d. Thiere. *Leipzig,* 1861.

81. Gudden, R. Beiträge zu den durch Parasiten bedingten Hautkrankheiten. *Archiv. f. physiol. Heilkunde. Stuttgart,* 1855.

82. Haller, G. Zur Kenntniss der Tyroglyphen und Verwandten. *Zeitschr. f. Wiss. Zool.* Bd. xxxiv. 1880.

83. Haller, G. Die Mundtheile und systematische Stellung der Milben. *Zool. Anz.* Jahrg. iv. 1881.

84. Haller, G. Ueber den Bau der vögelbewohnenden Sarcoptiden (Dermaleichiden). *Zeitschr. f. Wiss. Zool.* Bd. xxxvi. 1882.

85. Henking, H. Beiträge zur Anatomie, Entwicklungsgeschichte und Biologie von Trombidium fuliginosum. *Zeitschr. f. Wiss. Zool.* Bd. xxxvii. 1882.

86. Koenike, F. Zur Entwicklung der Hydrachniden. *Zool. Anz.* Jahrg. xii. 1889.

87. Kramer, P. Zur Naturgeschichte der Milben. *Archiv. f. Naturgesch.* Jahrg. xlii. 1876.

88. Kramer, P. Ueber Dendroptus. *Archiv. f. Naturgesch.* Jahrg. xlii. 1876.

89. Kramer, P. Ueber die Segmentirung b. d. Milben. *Archiv. f. Naturgesch.* Jahrg. xlviii. 1882.

90. Kramer, P. Ueber Gamasiden. *Archiv. f. Naturgesch.* Jahrg. xlviii. 1882.

91. Laboulbène, A., et Mégnin, P. Mémoire sur la Sphaerogyna ventricosa. *Journ. Anat. et Phys.* Année xxi. *Paris*, 1885.

92. Lohmann, H. Die Unterfamilie der Halacaridae Murr. u. die Meeresmilben der Ostsee. *Zool. Jahrb. Abth. f. Syst.* Bd. iv. 1889.

93. MacLeod, J. Communication préliminaire relative à l'anatomie des Acariens. *Bull. Acad. Roy. Sci. Belgique.* Sér. iii. Tom. vii. 1884.

94. Mégnin, P. Mémoire sur un nouvel Acarien de la famille des Sarcoptides, le Tyroglyphus rostro-serratus et sur son Hypopus. *Journ. Anat. et Phys. Paris*, 1873.

95. Mégnin, P. Mémoire sur le Hypopus. *Journ. Anat. et Phys. Paris*, 1874.

96. Mégnin, P. Sur les Métamorphoses des Acariens de la famille des Sarcoptides et de celles de Gamasides. *Compt, rend. Acad. Sci. Paris.* Tom. lxxviii. 1874.

97. Michael, A. D. British Oribatidae. Vols. i. and ii. *London. Ray Society*, 1883.

98. Michael, A. D. The Hypopus question, or the life history of certain Acarina. *Journ. Linn. Soc. Zool.* Vol. xvii. 1884.

99. Michael, A. D. Researches into the life histories of Glyciphagus domesticus and G. spinipes. *Journ. Linn. Soc. Zool.* Vol. xx. 1890.

100. Nalepa, A. Anatomie der Phytopten. *Sitzungsber. k. Akad. wiss. Wien.* Bd. xcv. 1887.

101. Nalepa, A. Beiträge zur Systematik der Phytopten. *Sitzungsber. k. Akad. wiss. Wien.* Bd. xcviii. 1889.

102. Neuman, C. J. Sur le développement des Hydrachnides. *Entom. Tijdsskrift. Stockholm.* Tom. i. 1880.

103. Nitzsch, C. J. Ueber die Fortpflanzung des Pteroptus vespertilionis. *Archiv. f. Naturgesch.* Jahrg. iii. 1837.

104. Robin, C., et Mégnin, P. Mémoire sur les Sarcoptides plumicoles. *Journ. Anat. et Phys. Paris*, 1877.

105. Winkler, W. Das Herz der Acarinen nebst vergleichenden Bemerkungen über das Herz der Phalangiden und Chernetiden. *Arb. Zool. Inst. Wien.* Bd. vii. 1888.

106. Winkler, W. Anatomie der Gamasiden. *Arb. Zool. Inst. Wien.* Bd. vii. 1888.

APPENDIX TO LITERATURE ON ACARINA.

I. Jourdain, S. Sur le développement du Trombidium holosericeum. *Compt. rend. Acad. Sci. Paris.* Tom. cxxv. 1897.

II. Kramer, P. Ueber die Typen der postembryonalen Entwicklung bei der Acariden. *Archiv. f. Naturgesch.* Bd. lvii. 1891.

III. Kramer, P. Zur Entwicklungsgeschichte und Systematik der Susswassermilben. *Zool. Anz.* Bd. xv. 1892.

IV. Lohmann, H. Die Halacarinen der Plankton-Expedition. *Leipzig*, 1893.

V. Schaub, H. von. Ueber die Anatomie von Hydrodroma. *Sitzungsber. k. Akad. wiss. Wien.* Bd. xcvii. 1888.

VI. Supino, F. Embriologia degli Acari. *Atti. Soc. Veneto-Trent* (2). Tom. ii.

VII. Trouessart, E. L. Sur l'existence de la parthénogénèse chez les Sarcoptides plumicoles. *Ann. Soc. ent. France.* Tom. lxiii. 1894. And *Bull. Soc. ent. Paris*, 1894.

VIII. Wagner, J. Zur Entwicklungsgeschichte der Milben, Furchung des Eies, Entstehung der Keimblätter und Entwicklung der Extremitäten bei Ixodes. *Zool. Anz.* Bd. xv. 1892.

IX. Wagner, J. Die Embryonalentwicklung von Ixodes calcaratus. *Trud. St. Peterb. Obshch.* Tom. xxiv.

CHAPTER XXII.

PENTASTOMIDAE.

Our knowledge of the *Pentastomidae* still rests principally on Leuckart's observations, supplemented by a few smaller treatises, and recently confirmed and amplified by Stiles.

1. Embryonic Development.

The eggs of *Pentastomum* are surrounded by two envelopes (Fig. 58 *A* and *B*, *h*). The early embryonic development takes place gradually as the ovum passes down the uterus. Cleavage is total (Leuckart, Macalister). The egg breaks up into a number of cells of about equal size, the further fate of which could not be ascertained. Macalister describes the formation of a blastoderm and a germ-band, but his statements are not conclusive. According to Leuckart, a germ-band is not formed. The embryo secretes a surface cuticle at an early stage, a disc-like thickening appearing on the dorsal surface of this cuticle. When the cuticle detaches itself from the embryo and forms a third envelope to the latter (Fig. 58 *A* and *B*, *eh*), it remains connected at this thickened disc (dorsal cone, *rz*). The chitinous integument also, which is now secreted as a covering for the embryo, is correspondingly thickened at this spot, and takes the form of a pit-like depression. The "dorsal cone," which at first connects these two chitinous thickenings, becomes constricted and broken through, but a trace of it is left attached to the embryo; this, in *P. taenioides*, is shaped like a raised cross situated in a cup-shaped groove (Fig. 58 *B* and *C*, *rk*). The remainder of the "dorsal cone" is retained on the detached integument as a circular thickening (the so-called facet, Fig. 58 *B*, *f*). This structure recalls the micropyle or the dorsal organ of the Crustacea, with which Leuckart has compared it.

A certain external similarity in structure is found between the so-called primitive tracheae of the Acarina and the dorsal cone of the *Pentastomum*; but these "tracheae" are paired and lie ventrally, so that there is no real agreement between them.

The early shedding of a cuticular integument within the egg, which must be regarded as a moult, recalls the formation of the deutovum-membrane in the Acarina (p. 96); similar processes occur also in the Crustacea (Vol. ii., p. 118).

Before the dorsal cone is broken through—*i.e.*, before the cuticular envelope is completely detached from the embryo—two pairs of truncated appendages have developed on the ventral side. These are limbs on which claws soon appear. A narrower posterior portion—the so-called tail—has, previous to this, become marked off from the compact trunk (Fig. 58 *A* and *B*), to the ventral surface of which it is applied. This caudal appendage is characteristic of the embryos of a few species of *Pentastomum*. In *P. taenioides* it is somewhat large (Fig. 58 *B* and *C*), while in *P. proboscideum* it is merely a small bifid appendage (Fig. 59, *s*). The embryo of *P. oxycephalum* has no caudal appendage, but presents a round posterior extremity. In this form the embryo leaves the egg (Van Beneden, Schubärt); it is therefore very unlike the parent in shape, and has to pass through radical transformations before attaining the adult form (Leuckart).

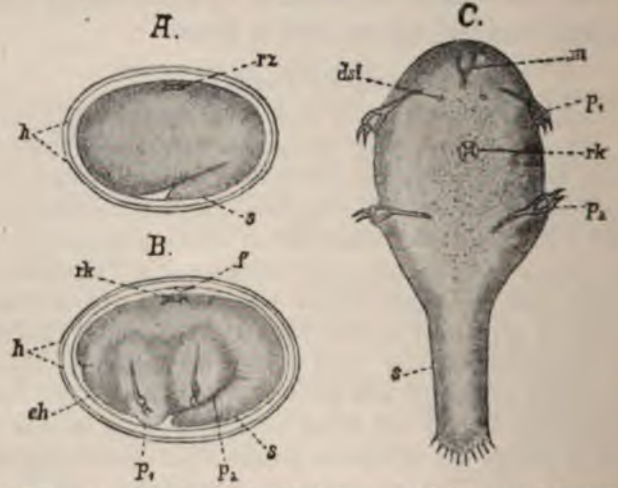

Fig. 58.—Embryos in the egg-integuments and free larva of *Pentastomum taenioides* (after Leuckart). *dst*, stigma of gland; *ch*, embryonic integument; *f*, "facet"; *h*, egg-integuments; *m*, oral plate; p_1 and p_2, truncated limbs; *rk*, dorsal cross (dorsal organ); *rz*, dorsal cone; *s*, caudal appendage. The boring apparatus of the embryo is not shown.

The Larval Development.

The further course of development is marked by the transference of the eggs into the intermediate host and the development of a four-limbed larva. The form whose ontogeny was examined by LEUCKART, *P. taenioides*, inhabits, in its sexual condition, the nasal cavity of the dog. The eggs are laid in the nasal mucus, and with this they reach the exterior. For the further development of the embryo an intermediate host is necessary. This, in the case of *P. taenioides*, is a rabbit, which, by swallowing the eggs, introduces them into its stomach, where the egg-integuments become detached and the larva set free. In *P. proboscideum* also (STILES), the early stages are similar to the above. The eggs of this form are found in the lungs of the boa constrictor; from the lungs they pass into the intestine, where they are found in quantities in the fæces, with which they leave the body. They, too, must be swallowed by an intermediate host in order to develop further. STILES was successful in introducing them into mice.

The larva, which has a blunt anterior, and a pointed posterior end, *i.e.*, which is supplied with a tail, has two pairs of truncated limbs, provided with chitinous claws furnished with a supporting apparatus (Fig. 58 *C*, and Fig. 59, *st*). The two claws are attached to a chitinous ring, and seem to be quite independent of the supporting apparatus. This structure suggests that the limb consists of a terminal, and a basal segment, the limb being thus regarded as two-jointed. STILES, who adopts this view, thought the limb more distinctly marked off from the body than did LEUCKART, who regarded it as consisting of one joint only.

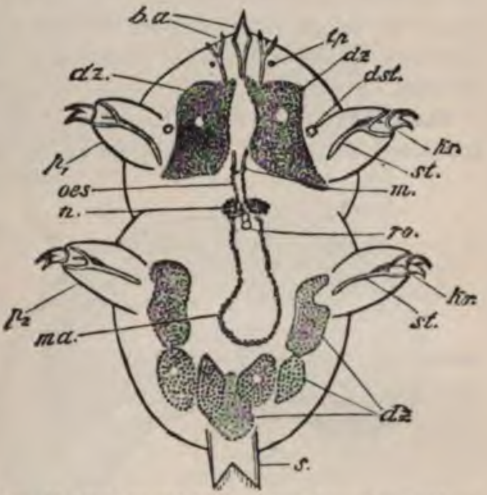

FIG. 59.—Quadrupedal larva of *Pentastomum proboscideum*, from the ventral side (after STILES). *ba*, boring apparatus; *dst*, stigma of gland; *dz*, gland-cells; *kr*, claws; *m*, mouth; *ma*, stomach; *n*, rudiment of the nervous system; *oes*, oesophagus; p_1–p_2, truncated limbs; *ro*, dorsal organ, seen through the transparent body; *s*, caudal appendage; *st*, apparatus for supporting the claws; *tp*, sensory papillae.

At the anterior end of the body lies a boring apparatus composed of several chitinous spines (Fig. 59, *ba*), which has been compared with the mouth-parts of the Arthropoda, especially with those of the Acarina, but such a comparison is hardly permissible on account of the position of this apparatus and its origin in front of the mouth; it must probably be regarded as a larval organ (Stiles). Near the boring apparatus are two small papillae, which have been regarded as tactile organs (*tp*).

The mouth, in *P. proboscideum*, lies somewhat far back, about on a level with the anterior truncated limb (Fig. 58, *m*). It is surrounded by a chitinous horseshoe-shaped band, and leads into a narrow oesophagus, which passes into a wider stomach. According to Stiles, there is no anus, although one is to be seen in Jacquart's not very accurate drawings. An accumulation of cells surrounding the oesophagus represents the rudiment of the nervous system (*n*). Stiles also found within the larva a large accumulation of richly granulated cells distributed in a definite manner, some of which are no doubt glandular cells. Two circular structures lying at the bases of the anterior extremities are regarded as the external apertures of glands (so-called stigmata of the glands, Figs. 58 and 59, *dst*).

The Encysted Larva. The larva which has become free in the intestine of the intermediate host, by the help of the boring apparatus at the anterior pole of the body and the limbs, traverses the wall of the intestine and passes into the other organs, *e.g.*, the liver, where it becomes attached and enclosed in a fibrous cyst derived from the tissues of the host. It here passes through a number of moults, during which it throws off the limbs and the boring apparatus. The caudal appendage also disappears, and the larva assumes a compact cylindrical form. Leuckart found, seven weeks after

Fig. 60.—Encysted larva of *Pentastomum taenioides* from the viscera of a rabbit, nine weeks after infection (after Leuckart). *a*, anus; *ag*, efferent duct of the genital gland; *dst*, glandular stigmata; *ed*, proctodaeum; *gd*, genital gland; *m*, mouth; *ma*, stomach; *n*, rudiment of the nervous system; *oe*, genital aperture; *oes*, oesophagus.

infection, in the cysts of *P. taenioides*, besides the worm-, or, rather, maggot-shaped larva, two cast integuments, on which could be distinguished remains of the embryonic chitinous structures, viz., the dorsal cross and the chitinous oral horseshoe-shaped band, and probably also the remains of the truncated limbs. Several further moults then take place, a long time being occupied by this development; five to six months, according to LEUCKART, pass before the larva of *P. taenioides* attains its full development in the intermediate host. The development of *P. proboscideum* is somewhat more rapid, but also occupies several months (STILES).

While the larva remains in the cyst, and during the course of several moults, the most important change which takes place is the development of the internal organs; the external form, however,

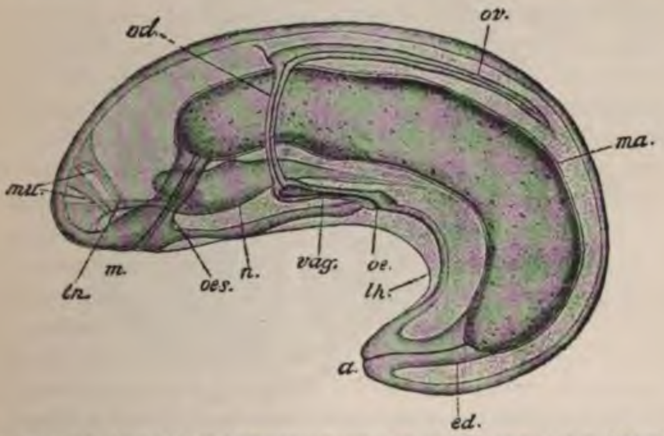

FIG. 61.—Encysted female larva of *Pentastomum taenioides* from the viscera of a rabbit, about four months after infection (after LEUCKART). *a*, anus; *ed*, proctodaeum; *lh*, larval integument (detached cuticle); *m*, mouth; *ma*, stomach; *mu*, retractor muscles of the pharynx; *n*, nervous system; *od*, oviduct: *oe*, genital aperture; *oes*, oesophagus; *ov*, ovary; *tn*, nerve running from the oesophageal ganglion to the tactile papillae; *vag*, vagina.

also undergoes a few changes, to be described below. The internal organs of the free larva, as far as could be ascertained, seem to pass direct into those of the encysted larva and of the sexually mature animal. The intestinal canal, which was not extensive in the free larva, widens and becomes differentiated into its separate regions, pharynx, oesophagus, and stomach. The latter soon becomes very large (Fig. 60, *ma*). It ends blindly posteriorly, and only becomes connected later with the proctodaeum (*ed*).

The accumulation of cells round the oesophagus present in the free larva (Fig. 59, *n*) during later larval life develops into the sub-oesophageal mass and the oesophageal ring, which represent the central nervous system of the adult. The sub-oesophageal mass, in early larval life, is much larger than in the adult animal, and occupies a considerable part of the ventral surface (LEUCKART, Figs. 60 and 61, *n*).

The rudiments of the genital organs can be recognised early, but, according to LEUCKART, it is at first impossible to distinguish the two sexes. A long, unpaired strand lying dorsally to the stomach, the germ-gland (Fig. 60, *gd*), forks anteriorly to form two strands (the rudiments of the efferent ducts, *ag*). These two strands embrace the anterior part of the stomach, and, after reuniting ventrally, open externally in the region of the ganglionic mass (*a*). There is very little difference in this respect in the male; the genital aperture in the adult male retains its primitive position in the anterior part of the body, not far behind the mouth. The genital aperture in the adult female is, however, found at the posterior end of the body, quite near the anus (Fig. 62, *oe*); and LEUCKART assumes that it has been thus displaced on account of greater growth of the part between it and the mouth taking place simultaneously with arrest of growth in the posterior region. Fig. 61 represents

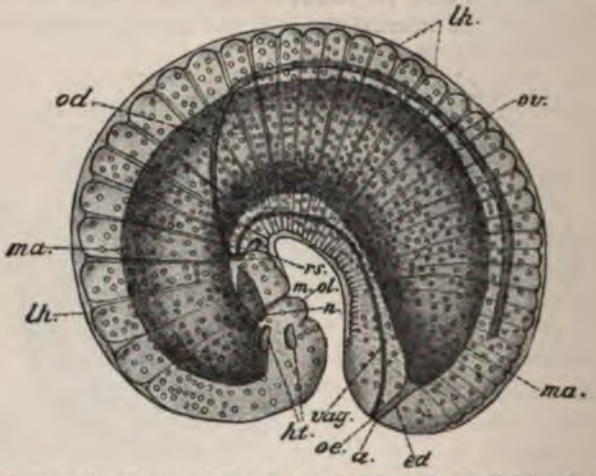

FIG. 62.—Encysted female larva of *Pentastomum proboscideum* (the so-called *P. subcylindricum*) from the viscera of a mouse, six and a half weeks after infection (after STILES). *a*, anus; *ed*, proctodaeum; *ht*, hook-sac; *lh*, larval integument (detached cuticle); *m*, mouth; *ma*, stomach; *n*, rudiment of the nervous system; *od*, oviduct; *oe*, genital aperture; *ol*, upper lip; *ov*, ovary; *rs*, receptaculum seminis; *vag*, vagina.

a transitionary stage, in which the genital aperture is already shifted further back than in Fig. 60. The differentiation of a vagina from the primitive genital duct has here already taken place. In Fig. 62, the genital aperture has already assumed its final position near the anus.

STILES speaks of a differentiation of the sexes at an early stage; but the stages described by him in *P. proboscideum* seem to us to be somewhat more advanced than those observed by LEUCKART in *P. taenioides*.

According to HOYLE, it appears that the genital glands may originally have been paired. If this were the case, we should have, in the fusion of the germ-glands to form a single organ, a process similar to that in the Acarina (p. 101). The position of the (female) genital aperture at the posterior end of the body, which is in opposition to what is usual in the Arachnida, might, according to LEUCKART's explanation, be regarded as secondary.

The body of the encysted larva after the first moults looks quite smooth, but later a series of rings make their appearance (Fig. 62). These first arise in the middle of the body, and spread anteriorly and posteriorly. These superficial markings cannot be regarded as equivalent to actual segmentation on account of their late appearance and their development. In some *Pentastomidae*, e.g., *P. protelis* (HOYLE), they are somewhat broad, and constrictions form between them, thus increasing the resemblance to a true segmentation. In *P. proboscideum* also such an appearance can be remarked, and is still more conspicuous in *P. taenioides*. In other *Pentastomidae*, raised rings are found like broad hoops round a barrel, separated by interspaces (VAN BENEDEN, JACQUART).

Small circular apertures in the chitinous integument are found distributed all over the surface of the body, and later, in consequence of the formation of rings, arranged in transverse rows upon it. These resemble the two glandular stigmata of the four-limbed larva (Fig. 62), and were regarded by LEUCKART as the apertures of integumental glands. A differentiation of the chitinous covering of the body which arises in later larval stages is found in the so-called circles of spines which appear at the posterior edge of each ring, and are characteristic of the fully-formed larva (Fig. 63, *st*). The larva of *P. taenioides*, which was formerly taken for a sexually mature form and called *P. denticulatum*, has the circles of spines specially well developed. They are probably of advantage to the animal in locomotion. Still more important aids in locomotion and attachment are the hooks—two pairs of claw-like chitinous structures (Fig. 63, *h*), which develop in two sac-like depressions of the integument in front of the mouth (Fig. 62, *ht*). The hooks have no connection with the truncated limbs of the larva, nor can they be regarded as limbs, as might appear from their origin as depressions and in front of the mouth. At a later stage they shift further back towards, or even behind, the mouth (Fig. 63). A further differentiation of the surface is found in the appearance of a large number of papillae arranged in pairs at the anterior end of the body (Fig. 63, *tp*), which have been considered tactile organs (Leuckart, Stiles).

The last larval form and its transference to the final host. While these external and internal ontogenetic processes have been taking place the body has lengthened, and has thus been forced to curl up in the cyst, within which the general form of the adult animal is reached. The larva (Fig. 63) now breaks through the cyst, and wanders away from the part hitherto inhabited by it, the circles of spines assisting it in this process. Should the intermediate host in which it lives at this time fall a victim to a beast of prey, the larva possibly passes direct out of the mouth of the latter into its nasal cavity, there, by renewed ecdysis, throwing off its spiny covering, and finally attaining the complete organisation of the sexually-mature *Pentastomum*. But if no such favourable opportunity is afforded the larva of reaching its final host, it becomes re-encysted within the body of the intermediate host. Encysted larvae which are swallowed by a beast of prey with the flesh of the host, and thus reach the intestine of the former, if sufficiently mature, break through the intestinal wall, and by active locomotion reach the respiratory tissues and the nasal cavity (Gerlach, Stiles).

Fig. 63.—Free larva of *Pentastomum taenioides* (the so-called *P. denticulatum*), from the liver of the rabbit or the nasal cavity of the dog (after Leuckart). *a*, anus; *d*, intestine; *h*, hooks; *m*, mouth; *st*, circles of spines; *tp*, tactile papillae.

3. General Considerations.

The most important point in the ontogeny of *Pentastomum* is the appearance of a larva furnished with two pairs of limbs. This larval form distinctly indicates that in *Pentastomum* we have an Arthropod, a fact which is not so evident from the organisation of the adult. It was this larval form above all that led to the classing of the *Pentastomidae* with the Acarina. The similarity would be still greater if a six-limbed larva also appeared in *Pentastomum*, as was maintained by DE FILIPPI. Unfortunately, but little reliance can be placed upon this otherwise important statement, as may be seen from a glance at his figures. A direct comparison of the *Pentastomum* larva with an Acarid larva is inadmissible on account of the absence of mouth-parts in the former. In this case degeneration may, indeed, have gone even further than in the Acarina, and it is possible that *Pentastomum* may be derived from forms resembling these latter animals. Certain Acarids, *e.g.*, the *Phytopta*, in which two pairs of limbs disappear, and in which the body is lengthened (pp. 107 and 108) might be regarded as indicating the possible line of origin of a form like *Pentastomum* (LEUCKART). But it must be expressly pointed out that there is no definite ground for this view, and that *Pentastomum* might, with almost equal justification, be derived from some other group of Arthropoda. Unfortunately, the organisation of the adult also fails to afford any definite clue, but only makes it clear that *Pentastomum* is a form much reduced by parasitism. Important systems of organs, such as the respiratory and excretory systems, which elsewhere, by their characteristic development, help to determine systematic position, are wanting. A distinct blood vascular system also is not developed. In the transversely striated musculature, on the other hand, we have an Arthropodan character, and it has already been pointed out that the genital organs can, perhaps, be interpreted in this sense. The ovary in its structure recalls that of the Arachnida, the eggs bulging out like follicles on its surface, and giving the organ an aciniform appearance.

LITERATURE.

1. BENEDEN, P. J. VAN. Recherches sur l'organisation et le développement des Linguatules (Pentastoma). *Ann. Sci. Nat.* (3). *Zool.* Tom. xi. 1849.
2. FILIPPI, F. DE. Nuova linguatula con embrioni di particolar forma. *Archiv. Zool., Anat. e Fisiol.* Fasc. i. Tom. i. *Genova,* 1861.
3. GERLACH, A. C. Pentastomum denticulatum bei zwei Ziegen. *Jahresber. d. k. Thierarzneischule zu Hannover.* ii. 1869.
4. HOYLE, W. E. On a new species of Pentastomum (P. protelis), from the Mesentery of Proteles cristatus, etc. *Trans. Roy. Soc. Edinburgh.* Vol. xxxii. 1887.

5. **Jaquart, H.** Mécanisme de la retraction des ongles des Felis et des crochets des Linguatules trouvées dans les poumons des serpents. *Journ. Anat. et Phys. Paris.* Année iii. 1866.
6. **Leuckart, R.** Bau und Entwicklungsgeschichte der Pentastomen. *Leipzig and Heidelberg.* 1860.
7. **Lohrmann, E.** Untersuchungen über den anatomischen Bau der Pentastomen. *Archiv. f. Naturgesch.* Jahrg. lv. 1889.
8. **Macalister, A.** On two new species of Pentastoma. *Proc. Roy. Irish Acad.* Ser. 2. Vol. ii. *Dublin,* 1875–77.
9. **Schubärt, T. D.** Ueber die Entwicklung des Pentastomum taenioides. *Zeitschr. f. Wiss. Zool.* Bd. iv. 1853.
10. **Stiles, Ch. W.** Bau und Entwicklungsgeschichte von Pentastomum proboscideum u. P. subcylindricum. *Zeitschr. f. Wiss. Zool.* Bd. lii. 1891. (This work contains a very complete bibliography of the Pentastomidae.)

APPENDIX TO LITERATURE ON PENTASTOMIDAE.

I. **Spencer, W. B.** The Anatomy of Pentastomum teretiusculum. *Quart. Journ. Micro. Sci.* (2). Vol. xxxiv.

CHAPTER XXIII.

PANTOPODA.

Oviposition and Care of the Brood. The Pantopodan female does not deposit her eggs in the usual manner, but transfers them to the male, who attaches them to his third pair of limbs, the so-called ovigerous limbs (Figs. 74, *3*, p. 157), and carries them about until the embryo is mature. The eggs are usually collected into large clumps, containing as many as 100. Several such clumps are found on one male, so that, if well laden, he may be found to carry 1000 eggs (DOHRN). Although in such cases, and generally among the Pantopoda, the eggs are very small, they are comparatively large in *Pallene* (0·25 mm. in diameter), being, for example, 125 times the size of an egg of *Phoxichilidium* or *Tanystylum* (MORGAN). *Pallene* carries only a few glutinous egg-clumps, each containing only two eggs (DOHRN). *Nymphon*, according to HOEK, has specially large eggs (in *N. brevicaudatum*, 0·5 to 0·7 mm. in diameter), but yet carries a great number. The large eggs are very rich in yolk, the smaller ones naturally have less yolk. The eggs are spherical, and each is surrounded by a delicate membrane (Fig. 64, *B*).

1. Cleavage and Formation of the Germ-Layers.

The cleavage of these eggs is total (DOHRN, HOEK, MORGAN); but those genera which have small eggs (*e.g. Phoxichilidium* and *Tanystylum*) show equal cleavage, those with larger eggs (*Pallene*, *Nymphon*) unequal cleavage (MORGAN).

Up to the present time but little has been known concerning the early ontogenetic processes in the Pantopodan egg. Many years ago (1843) KÖLLIKER gave an account of the total cleavage of the egg, and DOHRN has more recently described a few stages in the cleavage of the eggs of *Pycnogonum* that confirm the above conclusion. HOEK, in examining the Challenger material, found a few ontogenetic stages, which, however, could naturally only give a very incomplete idea of the development of the embryo. Hoek afterwards tried to complete his account by means of observations made on living specimens (*Pallene*, No. 7). Morgan next investigated the cleavage and formation of the germ-layers in these animals (Nos. 10 and 11), and in a more recent work (No. 12) he gives a detailed description of these processes in several Pantopodans. We shall thus have to rely chiefly on his account of these processes.

In *Pallene*, the first line of cleavage divides the egg up into two blastomeres, one of these being large, and the other only about a quarter of its size (Morgan). Each of the two spheres is again divided into two by a cleavage taking place at right angles to the first, so that two micromeres and two macromeres are now formed. The third line of cleavage is perpendicular to the two former lines, and gives rise to four micromeres and four macromeres. This stage is followed by one of eight small and eight large cleavage-spheres. From this point onward the micromeres and the macromeres do not divide at the same rate. At a later stage, sections present an appearance like that given in Fig. 65 *A*, except that the pole of the micromeres consists of smaller cells than are there figured. The cells are pyramidal, but their boundaries do not in all cases extend to the centre. We here find an indication of transition to the next important stage.

Unequal cleavage seems also to occur in the eggs of *Nymphon brevicaudatum*, which are rich in yolk, for, according to Hoek's figure (Fig. 2, Pl. xix., No. 6), one half of the egg at a late stage is composed of smaller cells than the other half.

The nuclei of the pyramidal cells, together with the surrounding protoplasm, shift to the periphery (Fig. 64 *A* and *B*), the boundaries of the blastomeres being retained to a certain extent (*dp*). To some degree, however, they disappear, this being specially noticeable towards the centre of the egg (*A* and *B*). The nuclei are surrounded by areas of protoplasm, which send out processes into the yolk. Since these complexes of protoplasm, increasing in number by division and shifting closer together, yield the blastoderm (Fig. 64 *C*), a stage like that seen in the Araneae is passed through, *i.e.*, the yolk-mass appears first divided up into pyramids which disintegrate later. According to Hoek's description, this breaking up of the yolk can still be distinguished in later stages after the blastoderm has formed (*cf.* figure of *Nymphon brevicaudatum*, No. 6, Pl. xix., Fig. 5). In the centre of the egg a cavity appears (Fig. 64 *A*, *fh*), which must be regarded as the cleavage-cavity. Its occurrence, however, does not seem to be constant (Morgan), and in any case it soon disappears again. This also, if proved to be correct, would constitute a certain analogy with a condition described for the Araneae (p. 39). In them also there is a transition from total to superficial cleavage. There is also a concentration of the blastoderm towards that pole at which later the first indications of the embryo appear (Fig. 64 *C*).

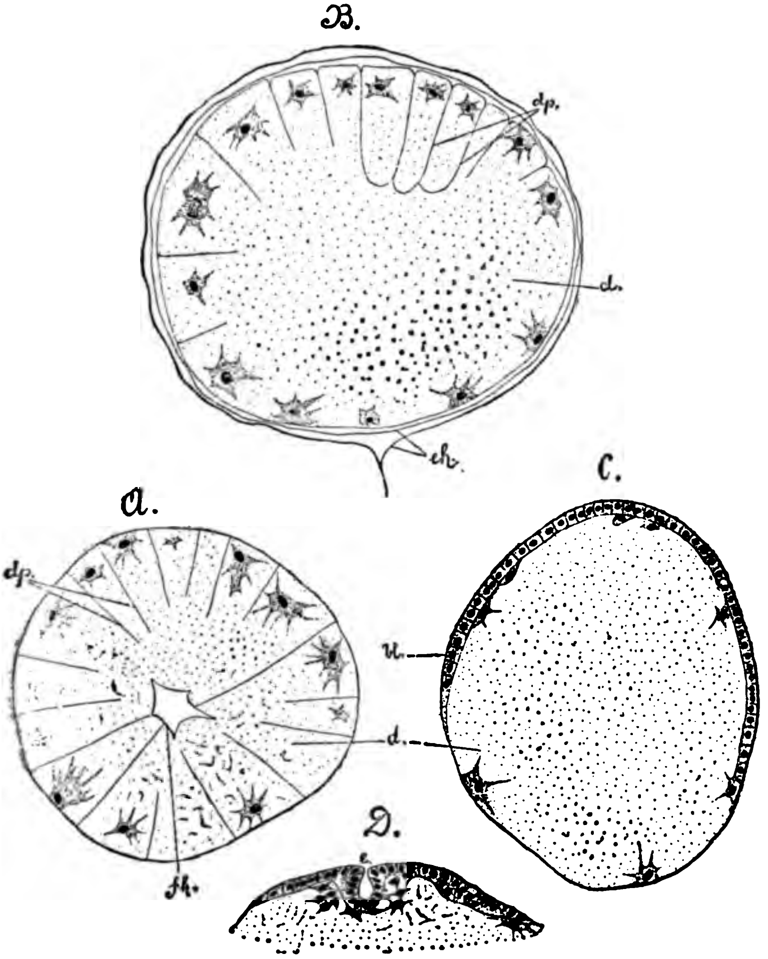

Fig. 64.—Sections through eggs of *Pallene* in various stages of blastoderm-formation (after Morgan). In *D*, an invagination (*e*) appears in the blastoderm, round which cells (probably the first mesoderm-cells) are given off. *bl*, blastoderm; *d*, yolk; *dp*, yolk-pyramids; *e*, aperture of the invagination; *eh*, external and internal integument; *fh*, cleavage-cavity (?)

The peripheral cells, which were also formerly present at the opposite pole (*A* and *B*), disappear.

At a time when the blastoderm only partly surrounds the egg, a few cells of amoeboid form are seen lying below it (Fig. 64 *C*). According to MORGAN, cells are given off first at the pole of the micromeres, and then at other parts of the periphery. These cells arise by division of the pyramidal blastoderm-cells in a tangential direction, a process which MORGAN, comparing it with the result of observations on other Pantopoda, considers to be one of delamination; a lower cell-layer forms, which is no doubt to be regarded as the entoderm. This view does not appear sufficiently supported by the facts as yet known, and MORGAN's observations have made possible another assumption with regard to the formation of the germ-layers. At the pole of the egg that is richer in cells a thickening appears, which has been compared by MORGAN to the primitive cumulus of the Araneid egg (p. 42). A depression then appears at this point (Fig. 64 *D*, *e*), and from this an active proliferation of cells takes place. MORGAN himself regards this as the formation of the mesoderm, and believes that some of the amoeboid cells which grow into the yolk are also of entodermal nature. The two germ-layers are not yet distinct from one another. In any case, the whole process shows great similarity to the formation of the germ-layers in the Araneae. Amoeboid cells are formed which grow into the yolk, and give rise later to the enteron. That some of the cells which originate near the invagination represent the rudiment of the mesoderm cannot be doubted. These cells soon increase greatly in number, and become arranged into two bands, the mesoderm-bands. The invagination which, on account of its relation to the formation of the germ-layers, might be regarded as the blastopore, is held by MORGAN to be the stomodaeum.

The two genera *Tanystylum* and *Phoxichilidium*, possess smaller eggs less richly provided with yolk, and these differ in their development from the larger eggs just described, inasmuch as they undergo equal cleavage, by means of which the egg breaks up into two, four, eight, and sixteen blastomeres of equal size. In consequence of this, the pyramidal cells of a later stage are also approximately equal in size (Fig. 65 *A*). The fact that the yolk contained in such an egg is smaller in quantity than in the other egg leads to a difference in the further development. An actual blastoderm is not at first formed, as in *Pallene*, but forms later by a process of delamination (Fig. 65 *B*). A cleavage-cavity also seems to arise, as may be seen in Fig. 65 *B*.

Each of the pyramidal cells divides tangentially into an inner and an outer cell, both of these cells then continuing to divide. The outer cells form at the periphery a regular layer, the blastoderm (Fig. 65 *C*, *bl*), while many of the inner cells lose their regular boundaries. A yolk-mass thus arises in which isolated cells lie (*C*, *d* and *z*). The inner cells, which were evidently the richer in yolk, have now fused to form a common mass. The embryo thus shows a condition similar to that of other Arthropoda, *e.g.*, the Araneae, there being a peripheral layer of cells (the blastoderm) and an inner yolk-mass with cells distributed in it. The latter, indeed, arise in a different way in the Pantopoda, as is shown in Fig. 65 *B*. The formation of the germ-layers could not be more exactly made out in eggs with equal cleavage, but MORGAN assumes that the enteron is formed from the inner cells (the entoderm). In these forms also, MORGAN early noticed a depression of the peripheral cell-layer, which, like the depression already described in *Pallene*, he regarded as the rudiment of the stomodaeum. This depression is triangular, a fact which has led to its being compared with the triangular stomodaeum of the Araneae.

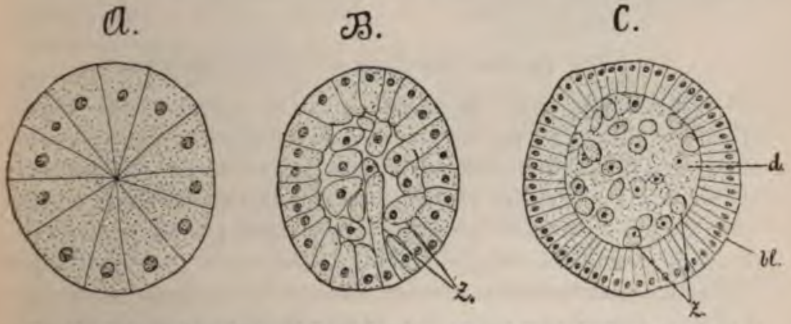

FIG. 65.—Sections through eggs of *Tanystylum* (*A* and *B*) and *Phoxichilidium* (*C*) in the final stage of cleavage (*A*) and in the stage of delamination and blastoderm-formation (*B* and *C*) (after MORGAN). *bl*, blastoderm; *d*, yolk-mass; *z*, the cells which become detached from the peripheral cells (blastoderm) and shift inward.

In view of the comparatively slight knowledge which we possess of the first ontogenetic processes in the Pantopoda, it would be too presumptuous to try to form further conclusions. It has already been mentioned that a certain agreement with the conditions in the Araneae exists. The splitting of the blastoderm into two layers maintained by MORGAN recalls the processes in the Pseudoscorpiones (p. 28); but these also are too little understood to allow of further comparison. The commencement of development and the further differentiation at the one pole might be compared to the formation of the germ-layers in the

Arachnida over a limited area of the blastoderm. MORGAN states very definitely that this budding-off of an inner layer of cells or multipolar delamination takes place in *Pallene* slowly, while the outer layer of cells is growing round the yolk; this we might perhaps refer to an ingrowth of cells with a circumcrescence of the yolk, and compare this process with the corresponding one in the Scorpion. It is advisable to direct the attention of future observers to this point. When the depression of the blastoderm described above appears, the entoderm, according to MORGAN, is already formed; the depression could not, therefore, be compared with the blastopore, although in other respects such a comparison is suggested, all the more so that MORGAN thinks that the mesoderm arises round this depression. The fact that other processes in the Pantopoda resemble those in the Arachnida is proved by the formation of a germ-band which, however, is much degenerated, but at the same time shows a certain resemblance to that of the Arachnida.

Eggs rich in yolk no doubt represent the more primitive condition in the Pantopoda, and the formation of a blastoderm (of the usual Arthropodan constitution) and of a germ-band must also be regarded as primitive. The reduction of the yolk probably had a great influence on the ontogenetic processes, which thus attained the condition in which they are now found (p. 154).

2. The Further Development of the Embryo.

Our knowledge of the development of the embryo and the origin of its organs is still very incomplete. The following accounts refer chiefly to *Pallene*, which was made the subject of careful investigation by MORGAN. We must, however, point out that *Pallene*, unlike other Pantopoda, remains within the egg almost up to the time when the adult form is reached (pp. 148 and 153).

When the invagination already mentioned has appeared on the thickened side of the blastoderm, other thickenings of the surface take place. Two of these are oval in form (Fig. 66, g), and lie in front of the triangular depression (m). These represent the rudiments of the supra-oesophageal ganglion. Extending posteriorly from the invagination are two rows of thickenings; these are the rudiment of the ventral chain of ganglia (g_{II}–g_{IV}); laterally to these the first indications of the limbs appear as distinct thickenings (Fig. 67, A). These rudiments, taken as a whole, form a band on the ventral surface of the egg, narrow anteriorly, but broader posteriorly, which may with safety be compared with the germ-band of other Arthropods. As the yolk-mass is not very large, the germ-band covers a great part of the egg. As the embryo develops further, it extends laterally, covering a still larger part, so that it can no longer be designated as a distinct germ-band, but rather as the embryonic rudiment surrounding the egg. During this process the embryo has also grown somewhat longer (Fig. 67 A).

The order of appearance of the limbs varies in the different forms. In *Pallene*, according to Morgan, the first to develop is the most anterior pair; these limbs lie near the mouth and are chelate, but their first appearance has not been observed with certainty. The next pair to arise is the fourth, and, in the gap which naturally occurs between these limbs, two pairs of ganglia are visible, those of the second and third pairs of limbs (Figs. 66 and 67 *A*). The fourth pair of limbs is followed by the fifth and sixth. The third pair develops later, but the second pair is altogether wanting in *Pallene*, and the seventh pair, like the third, appears a short time before the embryo leaves the egg-envelope. *Pallene* is thus seen to possess, as an embryo, all the limbs of the adult. In most other Pantopoda, however, this is not the case, only three pairs of limbs being usually developed within the egg-envelope. *Nymphon brevicaudatum* resembles *Pallene* in possessing all the limbs of the adult at the time of hatching (Hoek).

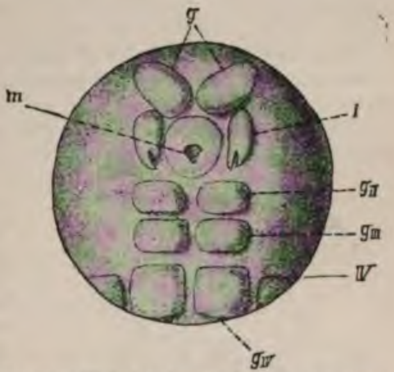

Fig. 66.—Superficial aspect of an egg of *Pallene*, showing the anterior part of the embryonic rudiment (after Morgan). *g*, rudiments of the supra-oesophageal ganglia; g_{II}–g_{IV}, ventral ganglia belonging to the segment carrying the second, third, and fourth pairs of limbs; *m*, mouth; *I*, first limb; *IV*, rudiment of the fourth limb.

While the limbs are appearing and gradually developing, the rudiment of the nervous system also undergoes further differentiation. Five pairs of large ganglia can be distinctly made out (Fig. 67 *A*). They belong to the segments carrying the second to the sixth limbs. It would be interesting to discover the relations of the ganglia which innervate the first pair of limbs to the supra-oesophageal ganglion, *i.e.*, whether they represent a post-oral pair of ganglia fused with the supra-oesophageal ganglion. The two anterior of these five pairs of ganglia approximate closely to each other later (Fig. 72 *B*), and in the adult these two ganglia, belonging to the second and third limbs, are united. The ganglia of the first three pairs of ambulatory limbs (Fig. 67 *A*), which appear early, are followed at a much later stage by those of the fourth pair (the seventh pair of limbs) and the abdominal ganglia.

In each of the ectodermal thickenings which represent the rudiments of the ganglia a pit-like depression appears (Fig. 67 *A* and *B*, *e*), round which the cells of the thickening show a regular epitheloid arrangement (MORGAN). An ectodermal depression thus takes part in the formation of the ganglion. The invagination closes later, but its cavity can still be recognised after the ganglion has shifted inward, and has lost its connection with the ectoderm (Fig. 68, *e*).

When the two anterior pairs of ganglia unite they appear as a single pair, in which, however, there are four pits, which proves that this one pair is composed of two.

MORGAN's statement as to the participation of ectodermal invaginations in the formation of the ventral ganglia is so definite, that we do not seem justified in doubting this fact (*cf.* Figs. 67 and 68). He himself compares these structures with the ventral organs of *Peripatus* (p. 189), and there is no doubt a certain similarity between the two; but it must be pointed out that the ventral organs are by no means in such direct connection with the ganglia as are the depressions in the Pantopoda.

A participation of an ectodermal invagination similar to the above in the formation of the brain cannot be established, although it is just here that we should expect it, when we take into account the cerebral pits in the Arachnida.

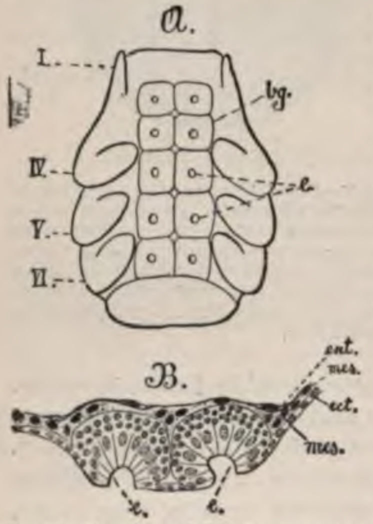

FIG. 67.—*A*, embryo of *Pallene empusa*, seen from the ventral side. *B*, part of a transverse section through the same, to show the paired depressions (*e*) on the ventral surface (after MORGAN). *I–VI*, limbs; *bg*, ventral chain of ganglia, the depressions (*e*) being visible in the ganglia; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm.

The development of the external shape of the body is completed by the addition of the missing appendages, the lengthening of the embryo, and the commencement of segmentation. The first pair of limbs shifts anteriorly and dorsally. At its base, the proboscis or beak appears to arise as an unpaired anterior outgrowth of the body, carrying the mouth at its extremity. At the posterior end of the body, the vestigial abdomen appears as a small pointed appendage, at the end of which the anus forms.

The first of the internal organs to claim attention is the enteron. The entoderm has become arranged into an epithelium surrounding the yolk-mass (Fig. 68, *ent*), and from this, diverticula, also filled with yolk, grow out at an early stage into the limbs (*di*). These are the intestinal caeca, which, in the larva (Fig. 72 *A*), as well as in the adult, run far into the limbs. This arrangement recalls that in *Chelifer*, where the yolk also extends far into the limbs (p. 29, and Fig. 16). This is also the case in the Acarina, and in the embryos of some Araneae, e.g., *Agalena* (Locy). This peculiar feature is known to be retained throughout life in the Pantopoda, in which the trunk is much reduced as compared with the limbs. These latter also contain the genital organs in the adult, and this explains the fact that a process of the mesoderm at an early stage runs between the ectoderm and the entoderm into the rudiment of the limb. According to Morgan, a cavity bordered by a mesodermal epithelium lies at the base of each limb, the mesodermal process extending from this point into the limb (Fig. 68, *mes*). Morgan does not hesitate to speak of the body-cavity of the limbs. In any case we thus have here the primitive segments which, taken together, represent the two already segmented mesoderm-bands. These latter, together with the rudiments of the ganglionic chain and the limbs on each side, form the germ-band (Fig. 66), although this is considerably reduced in accordance with the small size of the egg. As these mesoderm-bands develop at the thickened part of the blastoderm,

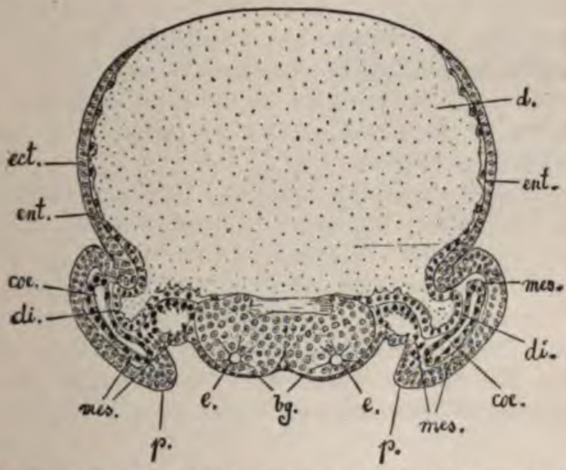

Fig. 68.—Transverse section through an embryo of *Pallene empusa* at a somewhat older stage than in Fig. 67 *A*. The ventral depressions (*e*) have closed (after Morgan). *bg*, ventral nerve-strand showing fibrous structure on the dorsal side; *coe*, mesodermal cavity in the limb; *d*, yolk; *di*, intestinal caeca of the limbs; *e*, the closed ectodermal invagination; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm; *p*, pair of ambulatory limbs.

the region beneath which the mesoderm extends may be regarded as the germ-band, the Pantopoda, as has already been pointed out, agreeing in this respect with other Arthropods.

Should the appearance of primitive segments and their extension into the limbs be confirmed, a strong resemblance to the Arachnida would be established. *Peripatus,* indeed, and many of the Insecta, show the same arrangement, but we do not feel confident in laying so much stress either on this or on the similarity to the ventral organ which **Morgan** specially points out. Transverse sections of embryos of *Pallene* (**Morgan**) and of *Nymphon* (**Hoek**) show unmistakable similarity to sections of a spider.

The further development of the mesoderm, its relation to the adult body-cavity, and the formation of the heart, have not yet been ascertained with sufficient certainty. The heart appears in the dorsal middle line after the mesoderm has already given rise to a number of schizocoele-like cavities. More accurate accounts of the participation of the primitive segments in these processes (the further differentiation of the mesoderm and the formation of the heart) would be of great interest.

The mesodermal tissue with its cavities increases in extent as the yolk-mass degenerates. The latter is absorbed by the surrounding entodermal epithelium. Yolk-cells do not appear to play any special part in this process, and may, indeed, be wanting. The enteron becomes connected with the stomodaeum, which is derived by **Morgan** from the invagination already mentioned as appearing very early. The proctodaeum does not appear until very late, when the seventh pair of limbs and the abdomen form.

The Form of the Larva and its Transformation into the Adult.

The Larva. Most of the Pantopoda develop through metamorphosis. The larvae usually have three pairs of limbs, but some leave the egg in a more advanced condition; the young *Pallene,* for instance, when hatched is provided with all the limbs of the adult, and this higher stage of development is also attained in the egg by a few species of the genus *Nymphon.* The various species of this genus differ from each other in this point; in some of them the larva, at hatching, has only four or five pairs of limbs (**Hoek**).

The many Pantopodan larvae that have been described differ only slightly from each other, and are easily derived from a larval form provided with three pairs of limbs. This form, which was first carefully examined by DOHRN, has a compact body (Fig. 69), sometimes almost square, or else rounded, seldom long or oval. The body is not externally segmented, although it carries three pairs of limbs; in this respect this larva bears a certain resemblance to the Crustacean *Nauplius.* It has been compared with the latter, but the resemblance is merely superficial.

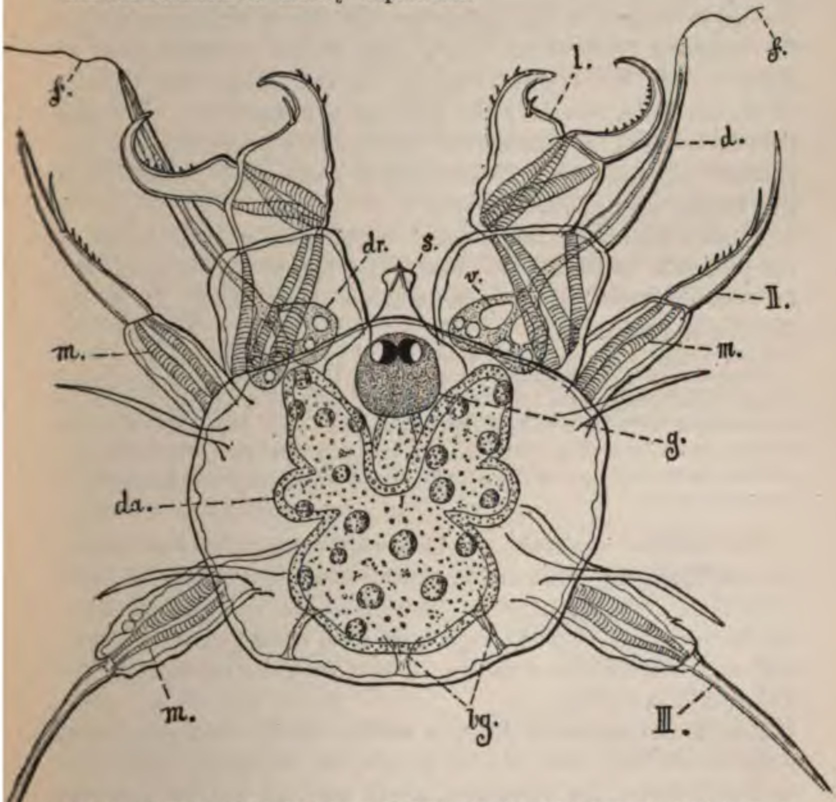

FIG. 69.—Larva of *Achelia laevis* immediately after hatching (after DOHRN). *I–III*, limbs; *bg*, strands of connective tissue; *d*, spine on limb *I* with gland (*dr*); *da*, enteron; *f*, filament of the glandular secretion; *g*, brain (with the eyes above it); *m*, muscles; *s*, proboscis; *v*, vacuoles in the gland.

The larva, as already stated, is supplied with three pairs of limbs. The most anterior limb has three joints, and is chelate. At its base it has a movable spine (Fig. 69, *d*), which, in other genera, is considerably longer than in the larva of *Achelia* depicted in Fig. 69. This appendage brings about a certain similarity to the biramose limbs of the Crustacea, but we would not lay any great stress upon this point. A tolerably large spine, comparable with that on the first limb, also occurs on the two following limbs (Fig. 69). That on the first extremity, however, is distinguished from the others by having at its point the aperture of a gland (*dr*). The fine filaments which can be produced through this aperture serve for attaching those larvae which, after quitting the egg-envelope and undergoing the first moult, fix themselves on the ovigerous limbs of the male. The second and third pairs of limbs possess hooks only (Fig. 69, *II.* and *III.*). The muscles of all the limbs, especially the first, are well developed. Whereas the first are used for fixation, and especially for prehension, the two posterior pairs are used for crawling and climbing. These larvae live among algae, Hydroids, etc.

Another feature of the external organisation of these larvae is the proboscis, or beak, which arises as a ventral conical outgrowth between the bases of the anterior limbs (Fig. 69, *s*). At its tip lies the oral aperture.

It appears as if the proboscis arose near the stomodaeum as an ectodermal outgrowth, although some have been inclined to attribute its origin to fusion of the upper lip with a pair of limbs (ADLERZ). It is impossible to decide whether we are justified in comparing it to the provisional proboscis of *Chelifer*, which it cannot fail to recall, on account of the slightness of our knowledge of this latter organ.

The intestine is already provided with outgrowths, the anterior pair of which are beginning to extend into the first pair of limbs (Fig. 69). From the intestine, fibres of connective tissue extend to the body-wall. The anus does not yet seem to be present (DOHRN), and no doubt does not appear until later with the rudiment of the abdomen (Fig. 71 *B*).

The nervous system of the larva consists of the supra-oesophageal ganglion and only two pairs of ganglia on the ventral side. Immediately above the supra-oesophageal ganglion lie the two eyes in close contact (Fig. 69). The manner in which these arise is of special interest, as it appears to offer a further point of agreement with the Arachnida.

The eyes, like the nervous system, attain full development during metamorphosis. The two eyes of the former stage are now joined by another pair. So as to understand how these develop we shall have to explain briefly the structure of the Pantopodan eye, which is as yet very insufficiently understood. These eyes, like those of the Araneae, consist of a corneal lens, a subjacent hypodermis (vitreous body), a thick layer of retinal cells, and a layer of pigment behind the whole. In the retina, the *cell nuclei lie in front of the rods; these latter therefore belong to the posterior part of the cells,* and thus come into direct contact with the pigment-layer (Fig. 70, *st*). *The nerve-fibres become connected, however, with the outer ends of the visual cells,* so that here also the same conditions prevail as are found in the posterior middle eyes and the lateral eyes of the Araneae (Fig. 34, p. 64). This last point, which seems to be implied in the description given by Hoek, has recently been established by Morgan (No. 12).

The ontogenetic stages, as well as the adult structure, closely resemble those of the Arachnida, as may be seen by comparing Fig. 70 with the ontogenetic stages of the eyes of the Scorpiones and the Araneae illustrated in Fig. 10, p. 14, and Fig. 35, p. 65. In Fig. 70, an invagination extending from one side below the hypodermis is suggested. The retina and the pigment-layer thus arise, and out of the superjacent hypodermis the layer forming the vitreous body, which secretes the lens on its outer side. An inversion thus takes place in the formation of the eye, and its innervation would be from the first explicable in the same way as that of the eye of the Araneae.

In earlier stages in the development of the eyes, an invagination is not so distinctly recognisable as in the eyes of the Araneae. The different layers of cells lie somewhat close to one another, and Morgan assumes that no actual (complete) invagination takes place, but rather that new cells are continually being added to the eye from the point of ingrowth, and that thus finally the layers, like those in the Arachnid eye, are formed (Fig. 70). A thickening of the hypodermis, which appears laterally to the eye, perhaps yields the new cell-material. This hypodermal thickening recalls the one found near the Crustacean eyes and those of *Limulus* (Vol. II., pp. 280 and 359).

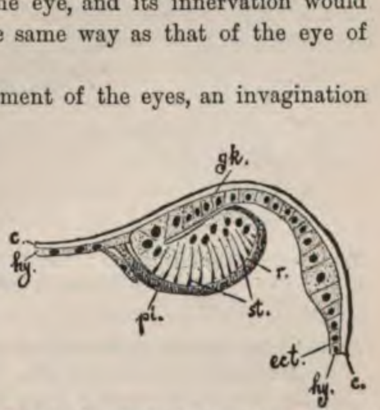

FIG. 70.—Longitudinal section through one of the posterior eyes of the larva of *Tanystylum* (after Morgan). *c*, cuticle; *ect*, *hy*, ectoderm (hypodermis); *gk*, vitreous body; *pi*, pigment-layer; *r*, retina; *st*, rods.

The development and the structure of the Pantopodan eyes suggests throughout a comparison with those of the Arachnida. Morgan's statement that the rods arise through fusion of the rods of two neighbouring cells, makes the similarity appear still more striking, and leads to the same conclusion in both cases; viz., to a derivation of these apparently simple eyes from compound eyes. Our knowledge of the eyes of the Pantopoda is, however, still too slight to allow of any definite conclusions; MORGAN even adopts an altogether opposite view, and explains the inversion which in all cases is present in these eyes, by the degeneration of the posterior part of an optic invagination and the better development of the anterior part. In this way he derives the inverted Pantopodan eyes from such simple eyes (ocelli) as those of the Insecta, being guided in this decision chiefly by a certain bilateral symmetry in the Pantopodan eye. But that method of development as it appears in the ontogeny of the eye, *i.e.*, the growth of the invagination towards one side, is merely a caenogenetic process, and serves for the quicker attainment of the structure now possessed by the adult eye. It has the significance of an abbreviated development. As a logical consequence of this view, a corresponding assumption must be made for the Arachnid eyes. We cannot here examine MORGAN's conclusions more closely, but refer to the original treatise and to our own view of the eyes of the Arachnida given above (p. 68). On the other hand, it must be mentioned that the description recently given by CLAUS (No. 2) of the origin of the median eye in the Crustacea, involuntarily recalls the condition of the eyes in the Pantopoda. The median eyes of the Crustacea are said by CLAUS to arise by inversion, and seem to have their elements arranged like those of the Pantopodan eyes. The rods lie on the inner side, directed towards the pigment-cup of the eye, while the nerve-fibres join them from the opposite side, where also lie the nuclei of the retinal cells.

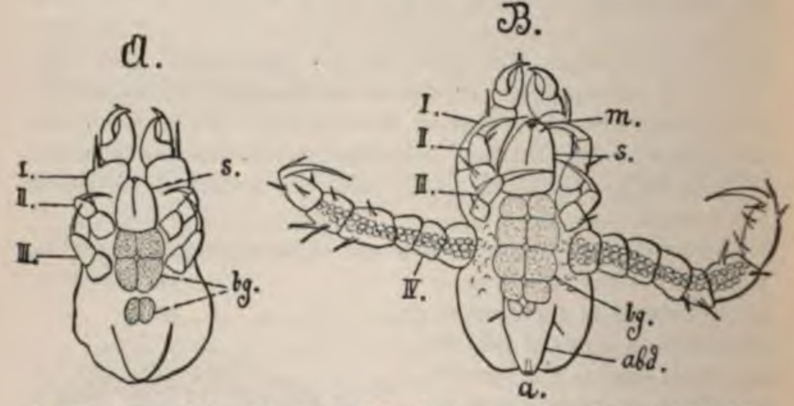

FIG. 71.—Larvae of *Tanystylum* in two different stages, seen from the ventral side (after MORGAN). *a*, anus; *abd*, abdomen; *bg*, ventral chain of ganglia; *m*, mouth; *s*, proboscis; *I–IV*, first four limbs.

The principal change which brings about the **transformation of the larva into the adult** is the formation of new segments at the posterior part of the body. The limbs already present either pass over directly to the adult, merely growing and developing further, or some of them, usually the second or third, and in many cases both of these or even all the three anterior pairs temporarily degenerate, the corresponding adult limbs growing out at the same points (DOHRN, HOEK). In *Pallene* the *second pair* is wanting, and does not even occur as a vestige, while in *Tanystylum* the *first pair* is wanting as a functional appendage, but appears ontogenetically as a well-developed pincer-carrying limb (Fig. 71 *A* and *B*), and only gradually degenerates in the later larval stages; it is still present in the adult as a small, vestigial two-jointed bud (MORGAN). The position of the second and third pairs of degenerated limbs is marked by the appearance of the apertures of what are presumably excretory glands (coxal glands). The tubular spine of the first limb, through which the above gland opens, is thrown off in one of the moults and gives place to an ordinary short spine. It has therefore the significance of a larval organ.

The first indication of the formation of new body-segments is, according to DOHRN, found in a paired swelling of the intestine behind the last of the larval limbs, accompanied by a bulging of the body-wall. At the same time, in the posterior part of the ventral surface, a thickening of the ectoderm appears which is the rudiment of a new pair of ganglia. The ectoderm begins to become wrinkled in the posterior part of the body and rises up above the newly-formed lower layer. The larva now moults, after which it is evident that a limb has appeared on the bulging of the body-wall just mentioned; into this limb an intestinal caecum is continued. It is thus clear that this is a new limb, which soon develops and becomes jointed (Fig. 71 *A* and *B*). The other limbs form in the same way. Only when the body thus lengthens do the three anterior pairs of limbs also take part in the transformation (DOHRN). The short abdomen arises as a posterior sac-like swelling, and the anus appears upon it (Fig. 71 *B*).

The transformation of the six-limbed larva just described takes place in some forms, as has already been mentioned, within the egg-envelope; *Nymphon brevicollum*, for example, leaves the egg when provided with five well-developed pairs of limbs (Fig. 72 *A* and *B*), and the first rudiments of a sixth pair. Other points of its organisation, especially the shape of the limbs with the intestinal caeca extending far into them, can be made out without further assistance from Figs. 72 *A* and *B*. The young of *Nymphon brevicaudatum* possess all the limbs at hatching (HOEK), and the same condition is found in the genus *Pallene* (DOHRN, MORGAN).

During metamorphosis, the rudiments of the genital organs which were not observed in the six-limbed larva become recognisable. In the larva with four pairs of limbs (Fig. 71 *B*), a compact mass of cells, the first rudiment of the genital gland, lies in the median line dorsally to the enteron, somewhat near the fourth pair of limbs (or first ambulatory limbs). The anterior end of this mass splits later into two parts, which grow out towards the bases of the limbs just mentioned. The posterior end of the germ-gland then splits in the same way, the genital tubes which run into the limbs thus arising. The wide tubular rudiment of the heart has formed at the anterior part of the body, also from mesoderm cells, dorsally to the genital rudiment, and thus directly beneath the integument.

FIG. 72.—Larvae of *Nymphon brevicollum* soon after hatching. *A*, dorsal, *B*, ventral aspect (after HOEK). *I-V*, the five anterior limbs; *bg*, ventral chain of ganglia; *d*, yolk-mass; *di*, diverticulum of the yolk-filled enteron in the limb; *g*, brain; *s*, proboscis.

The differences observed in *Pallene* and *Nymphon* give rise to the question as to which method of development is to be considered the more primitive among the Pantopoda; in this respect the appearance of larval organs and the casting of a larval integument, observed by DOHRN in *Pallene*, suggest that the direct development of this form must be regarded merely as an abbreviation of the indirect method of development, and that the latter is the more primitive. In consequence of the more complete development of the embryos in the egg the latter must have a richer supply of nutritive material. The large amount of yolk in the eggs of *Pallene* and *Nymphon* would, under these circumstances, appear as a later acquisition, and it then seems doubtful whether we ought to ascribe to the first ontogenetic processes of these eggs a truly primitive character, although we feel inclined to do so on account of the greater resemblance of their development to that of other Arthropoda.

The course of **development in Phoxichilidium** differs from that of other Pantopoda in that the form of the larva undergoes considerable degeneration before passing into that of the adult. This is connected with its parasitic manner of life.

On leaving the egg, the larva of *Phoxichilidium* possesses on the whole the organisation of the usual six-limbed Pantopodan larva, but is distinguished from the latter by the fact that the usually hook-like terminal joints of the two posterior pairs of limbs are much lengthened, and form long flagellae, which can coil up like tendrils (Fig. 73 *A*). These flagellae, which may be much longer than those represented in Fig. 73 (*e.g.*, in *Phoxichilidium femoratum*, (Hoek)), are probably used for attachment, the larvae winding them round the Hydroids (*e.g.*, *Hydractinia*, *Podocoryne*, *Tubularia*,

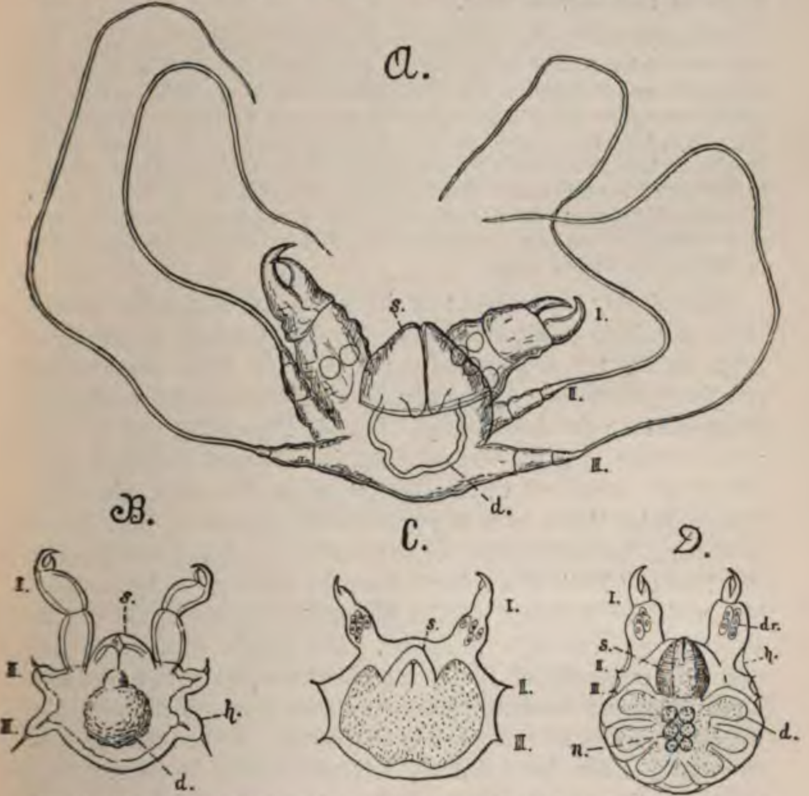

Fig. 73.—Various larval stages of *Phoxichilidium* (after Dohrn, Semper, and Adlerz). *A*, free larva with the tendril-like flagellae on the two posterior pairs of limbs (*II* and *III*). *B–D*, larval stages found in Hydroid polyps. (*A* is more highly magnified than the other figures.) *I–III*, limbs; *d*, intestine with its caeca; *dr*, glands of the first limb; *h*, larval integument in the act of becoming detached; *n*, ventral chain of ganglia; *s*, proboscis.

Plumularia), which are chosen by them as hosts. DOHRN assumes that the larvae, after attaching themselves to the Hydroids by the help of the flagellae, throw off during a moult the two posterior pairs of limbs that carry the latter, and pass through the oral aperture of the polyp into its gastral cavity. They are certainly found later in such a position, and here pass through the further stages of their development.

The tendril-like flagellae seem not to occur in all *Phoxichilidia*, for R. VON LENDENFELD has described a larva of *Ph. plumulariae* not distinguished in any way worth mentioning from the usual Pantopodan larva. This larva further differs from other *Phoxichilidia* in its manner of life; it does not penetrate into the polyps, but only attaches itself to them by the help of its pincers and by burying its beak in the host's body at the base of the head. The larva remains in this position until it has almost attained the form of the adult animal. We may gather from v. LENDENFELD's description that the further development of the forms discovered by him takes place as in other *Phoxichilidia*, for he also mentions a two-limbed stage.

It has already been stated that the larvae cast off the flagellae and limbs at ecdysis (SEMPER, DOHRN). The larva moults several times (Fig. 73 *B*), the second and third pairs of limbs degenerating completely (SEMPER); but, according to ADLERZ, some vestiges of the posterior pairs are retained (Fig. 73 *C* and *D*), and it is in place of these that the second and third limbs of the adult arise. The larvae, several of which often occur in one polyp, with their large anterior limbs, have a very peculiar appearance (Fig. 73) in this stage. In the following stages the limbs are found to degenerate still further (this is also evident from the figure given by ADLERZ), but, with the bulgings of the intestines, the rudiments of the posterior segments begin to appear. The ganglia of these develop and the outgrowths of the body-wall which yield the limbs soon appear (SEMPER, ADLERZ). These processes seem, on the whole, of the same nature as those before described. When three pairs of ambulatory limbs have formed, and the fourth is present as a rudiment, the young *Phoxichilidium* leaves the polyp and leads a free life.

4. General Considerations.

Although much has been written as to the relationships of the Pantopoda, these are still far from clear. The ontogeny of these animals, as far as it is now known, unfortunately throws little light upon the subject. In comparing the Pantopoda with other divisions of the animal kingdom, attention is turned chiefly to the Crustacea and the Arachnida. The form of the larva is of the greatest importance in a comparison with the former, while in comparing the Pantopoda with the Arachnida the shape of the adult receives more attention. It cannot be denied that the whole appearance of the Pantopoda suggests a certain similarity to the Araneae. But a nearer comparison at once reveals a difficulty, inasmuch as the Pantopoda possess one pair of limbs more than the adult Arachnid. An attempt has been made to overcome this difficulty by considering the first two pairs of limbs of the Pantopoda (Fig. 74, *1* and *2*) as equivalent to the chelicerae and the pedipalps of the Arachnida, and the third to the sixth limb of the former as equal to the ambulatory limbs of the latter (Fig. 74, *3–6*). The ovigerous limbs (Fig. 74, *3*) would thus represent the first pair of ambulatory limbs of the Arachnida, and the seventh limb would be the homologue of the first pair of abdominal limbs. In view of the fact that in the Insecta an abdominal segment is separated from the posterior part of the body, and may enter into the closest relation to the thorax, such a view might be defended. Those who adopt it consider that the addition of another pair of limbs to those already specialised for locomotion was determined by the withdrawal of the third limb from the ambulatory series for use in the care of the brood. According to this view, the four pairs of ambulatory limbs of the Pantopoda would not be homologous with those of the Arachnida. The last homology must, however, be regarded as possible, and in that case the loss of an anterior limb in the Arachnids would have to be assumed. It has already been pointed out (p. 111) that the rostrum has been conjectured to represent a pair of limbs.

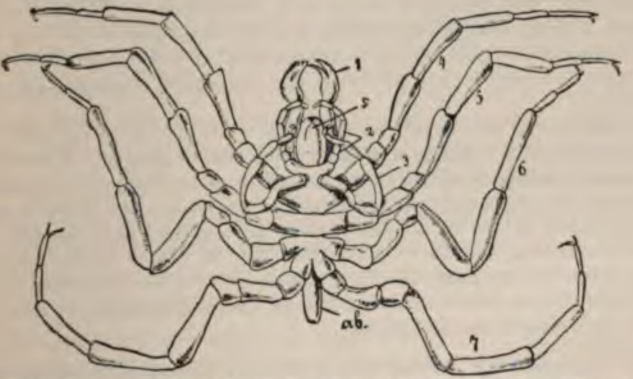

FIG. 74.—Male of *Nymphon hispidum* seen from the ventral side. The setae are omitted (after HOEK, from LANG's *Text-book*). *1–7*, limbs ; *ab*, abdomen ; *s*, proboscis.

In carrying further these attempts to homologise the limbs, this last assumption leads to certain difficulties as to the position of those now under consideration. A careful examination of the various views held on this subject, which are all more or less speculative, would lead us too far, but we must draw attention to the fact that the ovigerous limbs have by some been regarded not as independent limbs, but as belonging to the second limb. SCHIMKEWITSCH, who adopted this view (Nos. 14 and 15), in defending it laid weight on the fact that the rudiments of the pedipalps in the embryos of the Araneae are biramose (pp. 52 and 112). Each of the branches is said to give rise to a limb. This view is not supported by ontogeny, since, in the Pantopodan larva, the second and third limbs arise quite separately. Just as little does ontogeny support the view that the tripartite proboscis of the Pantopoda arises through the fusion of a pair of limbs with an (unpaired) upper lip. A third pair of limbs would then be added, for it cannot be assumed that the paired pieces are merely parts of one limb. The loss of two pairs of limbs by the Arachnida has even been suggested (CRONEBERG, p. 111). The ontogeny of the Pantopoda seems to show that the beak is, as DOHRN assumes, only an outgrowth of the lips of the stomodaeum. The number of the ganglia corresponds to that of the limbs, ADLERZ, indeed, finds (in the adult), besides the ganglia of the second and third limbs, another pair which innervates the proboscis. A final decision on this point will only be possible when the ontogenetic conditions are clearly established.

The first limb is innervated from the brain, while the second and third limbs receive their nerves from the first and second ventral ganglia. It would be of the greatest importance to make certain whether an originally post-oral ganglion unites with the brain, as in the Crustacea and the Arachnida. If this is not the case, the limbs lost in the Arachnida must be considered to be the first limbs of the Pantopoda, and their homologues must be sought in the conjectural rostral limbs of the Arachnida. It does not, however, seem probable that the first chelate limbs should be true antennae, and consequently not comparable to the chelicerae of the Arachnida.

We have already several times pointed out various resemblances between the development of the Pantopoda and that of the Arachnida, but these do not appear to us sufficient to lead to further conclusions as to the relationship of the two groups. MORGAN, chiefly on account of his ontogenetic researches, has recently spoken in favour of such a relationship. It appears to us that, in taking up this position, he was largely influenced by the structure of the Pantopodan eyes. But CLAUS has recently shown (Vol. ii., p. 167, and Vol. iii., p. 115) that the median eyes of the Crustacea also arise by invagination, and that their component parts apparently have the same position as those of the Pantopodan eyes (No. 2), so that in this character there is similarity to the Crustacea just as much as to the Arachnida.

In assuming the loss of an anterior limb, we are obliged to shift back any connection between the Pantopoda and the Arachnida to very early times in the history of the Arthropoda, before the

Arachnida arose from forms nearly related to the Xiphosura, for the Arachnida agree with the Xiphosura in many more points than with the Pantopoda. If we must remove the union of the two to such a remote period, the few points of comparison again lose their significance, seeing that they refer chiefly to the more highly developed forms and not to the lower forms. To derive the Pantopoda directly from the Arachnida, however, seems impossible, the latter having attained far too high a grade of organisation to allow of such a derivation.

Even if the Pantopoda were originally related to the Arachnida or some other segmented form, they have in their whole organisation become far removed from it, and have become markedly specialised. The decided preponderance of the limbs over the trunk, and the almost complete degeneration of the latter (Fig. 74) determined the displacement of the internal organs (intestinal caeca and genital glands) into the limbs. The opening of the genital organ on the second joint of the limbs is probably a consequence of this change, and thus has a secondary character. In those cases in which the genital apertures are found, not on several limbs, but only on the seventh pair, as in *Pycnogonum*, we might be inclined to derive this condition from that in *Limulus* and the Arachnida, in which the genital apertures lie in the first [second] abdominal segment, and to regard it as primitive, but such an assumption is not supported by any convincing evidence.

The reduction of the trunk as compared with the limbs becomes still more marked through the degeneration of the abdomen. The latter is merely a short, truncated appendage of the body (Fig. 74), but the presence of two pairs of ganglia (Dohrn) shows that it originally consisted of more than one segment. In *Ammothea* and *Zetes*, the abdomen shows externally a division into two parts, and in some other Pantopoda evidence of a larger number of segments (three to seven) is said to be forthcoming (Hoek, No. 7, pp. 453 and 454).

Should the Pantopoda prove to be connected at the roots with the Arachnid stock, they would thus in a certain way be related to the Crustacea. The latter, however, appear to us to be too far removed in structure to admit of any relation between the Pantopodan larva and the *Nauplius*. Those recent observers who have most thoroughly studied the ontogeny of the *Pantopoda* cannot find any close relation between the two. Hoek regards the larva as representing the primitive racial form, just as the *Nauplius* was formerly regarded. Dohrn considers it to be, like the *Nauplius*, a modified Annelid larva, and derives the Pantopoda from forms resembling the Annelida. Morgan, however, is unable to accept this conclusion, but regards it as a secondary larval form which can no longer be referred to the Annelidan larva. It seems to us that this last view might easily be reconciled with that of Dohrn.

Dohrn derives the Pantopoda from the Annelida, without relating them to the Crustacea and the Arachnida. He thus regards them as a distinct, independent group, and this is also Hoek's view (No. 7). Morgan, on the contrary, favours the relationship to the Arachnida, a view towards which Schimkewitsch also inclines (No. 15). He attributes the Pantopoda to the same racial form as the Arachnida, but believes that they branched off early and developed in a different direction. The most recent investigator of the Pantopoda, G. O. Sars (No. 13), does not connect them with either the Crustacea or the Arachnida, but wishes to make them into a separate class. In consequence of all these varying opinions we are unable to define with any degree of certainty the systematic position of the Pantopoda. On the whole, according to the present state of our knowledge, we shall do best to follow the conclusions of Dohrn (No. 4). If, notwithstanding this last decision, we have appeared to place the Pantopoda as next in order to the Arachnida, and to dwell on the possibility of the relationship of these two forms, this was done for practical purposes, since we should otherwise have been obliged to classify them in a less satisfactory manner, because they seem to show some slight similarity in their development, and a convergence in some anatomical points, to the Arachnida.*

LITERATURE.

Only a few of the many treatises describing the ontogenetic stages of the Pantopoda are here enumerated. The following literature, however, will afford further references.

1. Adlerz, G. Bidrag till Pantopodernas Morfologi och Utvecklings historia. *Bihang till k. Svenska Vetenskap. Akad. Handlingar.* Bd. xiii. Afd. iv. No. 11. *Stockholm*, 1888.
2. Claus, C. Ueber den feineren Bau des Medianauges der Crustaceen. *Anz. k. k. Akad. Wiss. Wien, Mai*, 1891. No. 12.

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* [Ihle (App. to Lit. on Pantopoda, No. I.) holds that it is impossible to ally the Pantopoda with the Arachnida or with the Crustacea, but thinks that the Myriopoda may be regarded as the ancestral stock. He lays special stress on the presence of a pair of abdominal appendages.—Ed.]

3. **Dohrn, A.** Untersuchungen über Bau und Entwicklung der Arthropoden. 2. Pycnogoniden. *Jen. Zeitschr. f. Naturw.* Bd. v. 1870.

4. **Dohrn, A.** Die Pantopoden des Golfes von Neapel. *Fauna und Flora des Golfes von Neapel.* Monographie iii. *Leipzig,* 1881.

5. **Faxon, W.** Bibliography to accompany "Selections from Embryological Monographs." Pycnogonida. *Bull. Mus. Comp. Zool. Harvard College.* Vol. ix. 1882. p. 247. (Contains the older bibliography.)

6. **Hoek, P. P. C.** Report on the Pycnogonida. *Voyage of H.M.S. Challenger. Zoology.* Vol. iii. 1881.

7. **Hoek, P. P. C.** Nouvelles Études sur les Pycnogonides. *Archiv. Zool. exper.* Tom. ix. *Paris,* 1881.

8. **Hodge, G.** Observations on a species of Pycnogon (Phoxichilidium coccineum) with an attempt to explain the order of its development. *Ann. Mag. Nat. Hist.* (3). Vol. ix. 1862.

9. **Lendenfeld, R. von.** Die Larvenentwicklung von Phoxichilidium plumulariae. *Zeitschr. f. Wiss. Zool.* Bd. xxxviii. 1883.

10. **Morgan, T. H.** Preliminary Note on the Embryology of the Pycnogonids. *Johns Hopkins Univ. Circulars. Baltimore.* Vol. ix. No. 80. 1890.

11. **Morgan, T. H.** The relationships of the Sea-spiders. *Biological lectures delivered at the Marine Biological Laboratory of Woods Holl. Boston,* 1891.

12. **Morgan, T. H.** A contribution to the Embryology and Phylogeny of the Pycnogonids. *Studies Biol. Lab. Johns Hopkins Uvniersity. Baltimore.* Vol. v. 1891.

13. **Sars, G. O.** Pycnogonidea. *Den Norske Nordhavs-Expedition 1876–78.* Bd. xx. *Christiania,* 1891.

14. **Schimkewitsch, W.** Étude sur l'anatomie de l'Épeire. *Ann. Sci. Nat.* (6). *Zool.* Tom. xvii. 1884.

15. **Schimkewitsch, W.** Les Arachnides et leurs affinités. *Archiv. Slaves Biol.* Tom. i. *Paris,* 1886.

16. **Semper, C.** Ueber Pycnogoniden und ihre in Hydroiden schmarotzenden Larvenformen. *Arb. Zool. Inst. Univ. Würzburg.* Bd. i. 1874.

APPENDIX TO LITERATURE ON PANTOPODA.

I. **Ihle, J. E. W.** Ueber die Phylogenie und Systematische Stellung der Pantopoden. *Biol. Centralbl.* Bd. xviii. 1898.

CHAPTER XXIV.

TARDIGRADA.

THE eggs of the Tardigrada are laid either singly (*Macrobiotus Hufelandi*) or several together, and are left in the cast-off skin of the mother. In the case of eggs laid singly, the egg-integument is thickly studded with small prominences which render its examination very difficult. When several eggs are laid together the egg-envelope is smooth and transparent. The species investigated by KAUFMANN seems to have been comparatively easy to study, and he was able to establish the fact that its cleavage is total and equal, as v. SIEBOLD had already stated. KAUFMANN followed the process of cleavage up to the formation of a morula stage composed of cells of about equal size. He then observed the separation of a peripheral cell-layer from the central mass, and the flexion of the embryo which supervenes. The concave side of the embryo seems to correspond to the ventral surface, for the limb-rudiments here arise on the two sides. Two pairs of prominences appear first; these are apparently the two anterior pairs of limbs, which are followed by the third and fourth pair. When the young leave the egg, they possess the full number of limbs and have the general form of the mother.

v. SIEBOLD's statement (No. 4, p. 553), that the *Emydiae* have only three pairs of limbs when they leave the egg, may be traced to a misunderstanding of DOYÈRE's account (No. 1). This author states that the limbs are here not fully developed, not that one pair is wanting. It does not appear from v. SIEBOLD's account that he himself investigated this point, which is of interest in connection with the comparison that has repeatedly been made between the Tardigrada and the Acarina.

The accounts of the ontogeny of the Tardigrada are unfortunately so scanty that we can hardly gain anything from them applicable to the whole group. We cannot even tell for certain if a blastoderm and germ-band develop, although this is probable. The armature of the mouth is evidently a product of the stomodaeum, as may be gathered from the study of the adult anatomy; mouth-parts (in the sense in which the term is used of the Arthropoda) apparently do not appear even as rudiments.* For this reason alone, the association of the Tardigrada with the Arachnida and especially with the Acarina, which has repeatedly been attempted, chiefly on account of the number of limbs, cannot be maintained. With regard to the number of their limbs, the Tardigrada cannot be compared with any other division of the Arthropoda, and the form of their limbs is so simple as to distinguish them in this respect also from all other Arthropoda. The segmentation of the body in the Tardigrada is peculiar, inasmuch as the abdomen is wanting and the anus lies in front of the last pair of limbs. In other points also the organisation of the Tardigrada shows peculiarities which distinguish it from that of other Arthropods; we may mention, by way of example, the unstriped muscle-fibres and the absence of special respiratory organs, and of a vascular system. For these and other reasons (*cf.* Plate, No. 3) we are led to consider the Tardigrada as a lateral branch of the Arthropod stock which separated from it near its root, and developed in a special and unique direction.

LITERATURE.

1. Doyère, M. Mémoire sur les Tardigrades. *Ann. Sci. Nat.* (2). Tom. xiv. *Zool.* 1840.
2. Kaufmann, J. Ueber die Entwicklung und systematische Stellung der Tardigraden. *Zeitschr. f. Wiss. Zool.* Bd. iii. 1851.
3. Plate, L. Beiträge zur Naturgeschichte der Tardigraden. *Zool. Jahrb. Abth. f. Anat.* Bd. iii. 1888.
4. Siebold, C. Th. von. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. *Berlin*, 1848. pp. 552 and 553.

APPENDIX TO LITERATURE ON TARDIGRADA.

I. Erlanger, R. von. Beiträge zur Morphologie der Tardigraden. Zur Embryologie eines Tardigraden, Macrobiotus macronyx. *Morph. Jahrb.* 1895. And *Biol. Centralbl.* Bd. xiv. and xv.

II. Kennel, J. von. Die Verwandschaftsbeziehungen und die Abstammung der Tardigraden. *Sitzungsb. Ges. Dorp.* 1891.

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* [Erlanger (App. to Lit. on Tardigrada, No. I.) has made an exhaustive investigation into the development of *Macrobiotus macronyx.* He finds that cleavage is total and equal and results in the formation of a long, oval blastula with a cleavage-cavity; an invagination-gastrula arises whose blastopore, which occupies the position of the future anus, soon closes; a very short proctodaeum is formed, and the archenteron divides into a pharynx, gullet, and stomach; four pairs of enterocoeles form, and the embryo becomes divided into a head and four thoracic segments. The head-coelom enters into connection with the first pair of appendages; the coelomic pouches of the second and fourth thoracic segments enter into relation with the remaining appendages, while that of the third segment gives rise to the gonads and (?) to a pair of enteric glands. The oral papillae, the salivary glands, the nerve-ganglia, and the eyes all arise from the ectoderm. Erlanger regards the head and first two thoracic segments as the cephalo-thorax; the third and fourth segments as the abdomen, behind which is a transitory post-abdomen.—Ed.]

CHAPTER XXV.

ONYCHOPHORA (PERIPATUS).

Structure of the Eggs and Nourishment of the Young by the Mother. The eggs of *Peripatus* pass through their development in the uterus, but there is considerable variation in this respect in the different geographical species. This point has been carefully investigated up to the present time in *P. novae-zealandiae* (Australia), *P. capensis* and *P. Balfouri* (Africa), and *P. Edwardsii*, *torquatus*, and *Imthurni* (South America). These species differ even in the size of the egg and of the mature embryo. The oval eggs of *P. novae-zealandiae* are 1·5 mm. long and 1 mm. broad, and the young which hatch from them are not much larger than the eggs themselves; the eggs of *P. capensis* and *P. Balfouri* are 0·4–0·6 mm. long, but the newly-hatched young of the former has a length of 10–15 mm., and that of the latter is about half as long. In *P. Edwardsii* the mature embryo attains the length of 22 mm., *i.e.*, a third of that of the mother, while the egg is here only 0·04 in diameter. The species in which the young are largest at birth have thus the smallest eggs, and *vice versâ*. The explanation of this striking fact is to be found in the circumstance that in the South American species the egg or embryo remains in close connection with the mother, and is nourished by means of a "placenta and an umbilical cord" (Fig. 88, p. 179).[*] This accounts for the extraordinarily small size of the eggs in this case, and for their being devoid of nutritive material. In the African species the eggs are larger, but the newly-hatched young are smaller than in *P. Edwardsii*, there being no correlation between the size of the egg and that of the embryo, the latter, although not

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[*] We are here following the definite statements of v. Kennel (No. 4), which rest upon his own observations, although we are aware of the statements made by Hutton (No. 3) as to the size of the newly-hatched young of *P. novae-zealandiae*. These, according to this latter author, measure from 8 to 10 mm. Since v. Kennel's statements were not contradicted by the more recent observers of the *Peripatus* of New Zealand, we must assume that the difference is only apparent, and that the large size of the embryo as compared with that of the egg must be traced not to its greater mass, but rather to its increase in length and to its extension after leaving the egg.

attached to the wall of the uterus, is nevertheless nourished by fluid yielded by that organ. In the New Zealand species, such nourishment from the mother is not needed, since the embryo is not essentially larger than the egg. In this case, therefore, the material for the development of the embryo must be contained in the egg itself. It is actually found that the egg of *P. novae-zealandiae* is very rich in yolk, as are those of most Arthropods. The general course of its cleavage also agrees with what is found, for instance, in the Insecta. Considering the close relationship of *Peripatus* to the Arthropoda, which can hardly be disputed, it seems likely that the condition of the egg of *P. novae-zealandiae* is the primitive condition.

It is probable that *Peripatus*, like the terrestrial Arthropoda generally, originally produced eggs rich in yolk which it laid. This state of things is recalled by the presence of a firmer egg-envelope in *P. novae-zealandiae*, already pointed out by SEDGWICK (No. 11); the laying of eggs not fully developed also in this same species points in this same direction, even though we find that eggs laid thus early do not attain full development (HUTTON, No. 3). The capacity for developing the eggs within the body must have been secondarily acquired. The egg of the New Zealand species, which is rich in yolk and develops within the uterus, represents the first step in this newly-acquired course of development. An accumulation of nutritive material in an egg which develops within the uterus is unnecessary, and this is opposed to the assumption that in *P. novae-zealandiae* we have a specialised form in which the egg has been secondarily supplied with yolk. A further step in adaptation would be represented by *P. capensis*. The eggs here show a spongy structure as if penetrated by fluid yolk, and this, as well as the method of their development, seems to indicate that they to a certain extent represent a degenerate condition of eggs originally rich in yolk. Isolated granules of yolk also appear in these eggs, and in *P. Balfouri* the egg is still somewhat rich in definite yolk-masses. In the species found in the West Indies, the nourishment of the embryo by the mother has become so complete that no trace of the former rich supply of yolk remains in the eggs which have become extraordinarily small. These biological conditions naturally find expression also in the method of development of the different species.*

1. Cleavage and Formation of the Germ-Layers.

Although the early development, the cleavage and the formation of the germ-layers, has repeatedly been investigated in different species, our knowledge of these processes still remains very incomplete. This fact is accounted for by the

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* [WILLEY (App. to Lit. on Onychophora, No. II.), from the study of the egg of *P. novae-britanniae*, has come to conclusions which are exactly the reverse of those given above; and here he is in agreement with v. KENNEL, who believes that the ancestral *Peripatus* discharged a small yolkless egg into the water, and that the intra-uterine development was concomitant with the adaptation of the parent to a terrestrial existence. These authors then conclude that the development of yolk in the eggs of *P. novae-zealandiae* is quite a secondary condition, which, WILLEY believes, culminates in the return to the oviparous condition observed by DENDY (App. to Lit. on Onychophora, No. I.) in *P. oviparus*, which WILLEY regards as a secondarily acquired habit.—ED.]

difficulty of obtaining material, for the eggs, taken from living animals brought to Europe, were sometimes in such a bad condition (Sedgwick, No. 10, Pt. I., Figs. 7–13), that the researches made on them could not be of any great value. Some of the observations also are incomplete, or, as in the case of the South American species examined by v. Kennel, important differences of opinion arise between observers (v. Kennel and Sclater) which can only be finally settled by further research. A connected description of the first ontogenetic processes and their inter-relationships in the various species is as yet impossible. We shall first consider the development of *P. novae-zealandiae* which, for the reasons given above, we regard as showing the most primitive condition, and then deal with the African species. The South American species, from what we as yet know of them, seem to claim a position distinct from the others.

Peripatus novae-zealandiae.

Cleavage is here superficial. The eggs are rich in yolk, and the cleavage-nucleus appears to have a peripheral position. Its division gives rise to nuclei surrounded by islands of protoplasm; these for the most part also lie peripherally, but single nuclei shift towards the centre of the egg, as may be seen in the figures given by Lilian Sheldon (Fig. 75, No. 12)

It is no doubt due to the distribution of the nuclei in the yolk that this latter breaks up to some extent into distinct rounded areas (Fig. 76 *A*), although Lilian Sheldon was not always able to prove that these were regular yolk-pyramids either in origin or form. This breaking up of the yolk led former observers (Hutton, No. 3, v. Kennel, No. 4, Pt. I.), who could only make observations on insufficient material, to the conclusion that the egg of *P. novae-zealandiae* underwent total cleavage.

75.—Section through the egg of *P. novae-zealandiae* (after L. Sheldon). In the yolk are the nuclei surrounded by areas of protoplasm.

According to the description given by L. Sheldon, the cleavage-nucleus and the nuclei which first arise seem to lie on the later dorsal side and opposite to the point at which the blastoderm forms. These nuclei increase in number and form a peripheral accumulation (protoplasmic or polar area, Fig. 76 *A*, *a*), starting from which, circumcrescence of the yolk takes place (formation of the blastoderm). The active increase in number of the cells and their constant shifting towards the periphery, leads to the almost complete circumcrescence of the yolk as far as a point lying almost opposite the original accumulation of nuclei, where the yolk remains uncovered. Here an ingrowth of cells then takes place, the appearance of an invagination being thus produced (Fig. 77 *A* and *B*). The point of invagination is the blastopore (*bl*), and the base of the depression is formed of yolk in which nuclei can be recognised (Fig. 77 *B*). The germ-layers do not yet appear to be differentiated from the cell-mass surrounding the blastopore, which represents the rudiment of the germ-band. Miss SHELDON seems to assume that the part of the cell-mass underlying the superficial cell-layer (or ectoderm) yields chiefly mesoderm, while the entoderm arises from the cells lying in the yolk, and which, according to Miss SHELDON, arise and multiply by a process of free nuclear formation (?), as she was unable to observe any karyokinesis.* The blastopore lengthens later and then resembles a small groove, the base of which is formed by the nucleated yolk. We here have a resemblance to the condition in *P. capensis* illustrated in Fig. 84 *A*.

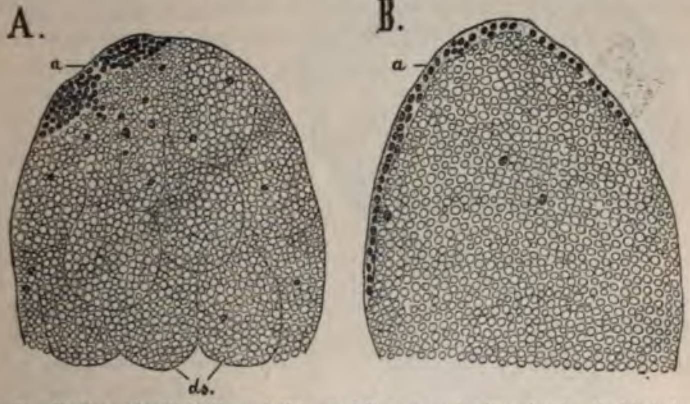

FIG. 76.—Portions of sections through the egg of *P. novae-zealandiae*, showing the blastoderm-formation (after L. SHELDON). *A* shows the "polar area" and the cleavage of the yolk. *B*, the commencement of the circumcrescence of the egg. *a*, "polar area"; *ds*, "yolk segments."

As far as we can gather from the description of L. SHELDON, the process of circumcrescence is regarded by her as an epibolic gastrulation. The yolk-mass, with the nuclei contained in it, would correspond to the entoderm. A study of the figures, however, has compelled us to form another conclusion, which gains in probability from the fact that we are here dealing, as in the case of many

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* [It is extremely doubtful if there is such a process as free nuclear formation. All recent research on nuclei tends to prove that *every nucleus originates from a pre-existing nucleus* either by mitotic or amitotic division.—ED.]

Arthropods, with an egg very rich in yolk. Whether the blastoderm is really formed by circumcrescence of the egg starting from one pole, or whether the nuclei contained in the yolk, by shifting to the surface, help to form it, the peripheral accumulation of cells which recurs in the same way in various stages claims identification with the cell-accumulation in the neighbourhood of the blastopore (*cf.* Figs. 76 and 77). We should then not be obliged to assume gastrulation through epibole, which is unusual in eggs so rich in yolk, but should rather assume that at the point where this cell-accumulation is found a depression (invagination) occurs (Fig. 77 *B*). Whether the base of this depression is formed of yolk (containing nuclei), or whether a closed archenteron is present, would in this case still have to be decided. If the blastopore lengthened later (*cf.* also *P. capensis*) there would be a resemblance to the gastrulation of the Insects. In these latter, as in *Peripatus*, the mouth and anus show a connection with the two terminal points of the long blastopore.

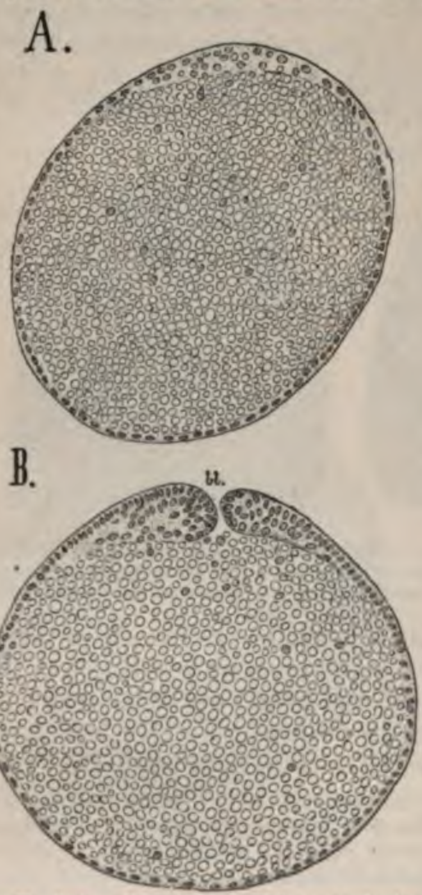

FIG. 77.—Sections through the egg of *P. novae-zealandiae*, showing the formation of the blastoderm and invagination (after L. SHELDON). *bl*, blastopore.

In this conception of the cleavage and formation of the germ-layers, it may be noticed that the invagination apparently takes place at the animal pole of the egg. But if it is remembered that in *P. capensis* the brain arises in the immediate neighbourhood of the blastopore, it will be seen that we must rather regard this as a shifting of the vegetative pole, or the region of entoderm-formation, towards the animal pole, than as a gastrulation at the animal pole. The same is the case in the Insecta and in many Crustacea (Vol. ii., pp. 141 and 142). The view here adopted receives a general support from the conditions in the Crustacea, in which the circumcrescence of the yolk (or the formation of the blastoderm) takes place from one point, gastrulation afterwards occurring in that region (Vol. ii., p. 115). We are unable in the present state of knowledge to obtain any light upon these processes from the ontogeny of *P. capensis*.

Peripatus capensis.

In consequence of the eggs of *Peripatus capensis* being poor in yolk, their cleavage is apparently total. According to SEDGWICK, an animal pole (corresponding to the later dorsal side) can be distinguished from a vegetative pole. Two meridional furrows divide the egg into four blastomeres of equal size, each of which contains a portion of the animal and a portion of the vegetative protoplasm. These cleavage-planes are said not to cut through the whole egg, the blastomeres being united centrally. At a later stage, an equatorial furrow separates the smaller ectoderm-cells (animal pole) from the larger entodermal blastomeres. At the close of segmentation, the cells are very loosely connected, the smaller ectoderm-cells are closely applied together, while the larger entoderm-cells are amoeboid and scattered irregularly within the egg-membrane. The stage which follows may roughly be compared with the blastula. The entoderm-cells draw together and lie directly beneath the smaller ectodermal cells, which then grow round the entodermal elements, a solid (and therefore epibolic) gastrula being thus formed in the course of further development. The archenteric cavity is said to arise in the entoderm through the formation of "vacuoles"! It opens externally at the point which has remained unaffected by the circumcrescence, and thus corresponds to the blastopore. Behind this, an increase in number of the cells of the superficial layer takes place, which leads to a thickening of this layer and then to a separation of the lower layers, that have thus arisen, as the mesoderm. During the lengthening of the blastopore, which soon occurs, and the simultaneous increase in length of the whole embryo (Fig. 84 *A*), the mesoderm grows forward on both sides of the blastopore and thus yields the mesoderm-bands. The rudiment of the germ-band is thus produced (SEDGWICK).

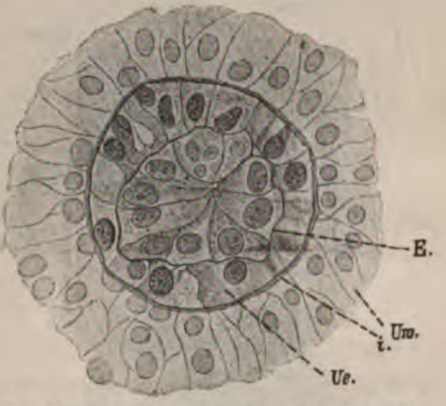

FIG. 78.—Section through a 16-celled embryo of *P. Edwardsii* lying in the uterus (after J. v. KENNEL). *E*, embryo; *i.Uw*, inner wall of the uterus; *Ue*, uterine epithelium.

In the better preserved eggs figured by SEDGWICK, large cavities can be seen in the protoplasm, and this leads us to conjecture that, in the normal condition, the eggs might be filled with a more or less fluid mass of yolk. These spaces in the body of the egg are very large, occupying a large part of its interior, so that, when the very unsatisfactory condition of the material investigated is taken into account, we are led to the conclusion that the cleavage may in this case also be superficial. The cavities in the blastula-stage just described would then be filled with yolk, and the gastrula would perhaps be formed by invagination, as was conjectured in the case of *P. novae-zealandiae.* As we have not personally examined these eggs, we do not feel justified in giving definite expression to this view, but we cannot refrain from making a conjecture which appears to us so probable. There would in this case be a certain similarity between the African and the New Zealand species, especially as it may with probability be assumed that eggs poor in yolk are to be derived from eggs rich in yolk. This last view is held by SEDGWICK himself, and in a later treatise (No. 10, Pt. iii.) he calls the egg of *P. capensis* meroblastic, because of the central connection mentioned above as existing between the blastomeres.

The American species.

On account of the small size of their eggs and the connection between these and the wall of the uterus, the American species differ entirely in their development from the forms we have so far considered.

The small eggs, poor in yolk, undergo a total and apparently fairly regular (equal) course of cleavage. The embryo, even at this early stage, appears to obtain nourishment from the uterus, for it increases in size in a marked manner (v. KENNEL). When it has reached the 32-cell stage, it forms, according to v. KENNEL, a solid cell-mass, completely filling the narrow lumen of the uterus, and thus in close contact with the inner surface of the uterine epithelium (Fig. 78). This

FIG. 79.—Sections through embryos of *P. Edwardsii* together with the uterine wall (after J. v. KENNEL). *E*, embryo; *am*, amnion; *a.Uw*, outer wall of the uterus; *i.Uw*, inner wall of the uterus; *Ue*, uterine epithelium [embryonic derivative, SCLATER and WILLEY].

latter at first consists of very deep cells which, however, under the influence of the growing embryo, seem to flatten. The embryo then, according to v. KENNEL, enters into direct connection with this epithelium, this change being accompanied by a peculiar alteration in the shape of the former. The embryo, which is said to give off fluid and to decrease in size, becomes applied to the epithelium as a lenticular cell-mass (Fig. 79 *A*). The figures show the close nature of the connection between the embryo and the epithelium, the latter may, indeed, occasionally become detached from the wall of the uterus, and may surround the embryo as a special layer (Fig. 79 *B*, *Ue*). The central part of the embryo now rises from the surface of the uterus, while the edges, which still remain in contact with the latter, become somewhat approximated through these changes; the embryo thus assumes the form of a cap open towards the surface of the uterus (Fig. 79 *B*). From the surface of the embryo a few amoeboid cells become detached; some of these become applied to the uterine epithelium and, finally, these amoeboid cells unite and give rise to an envelope which surrounds the whole embryo, and which has been termed the amnion or serosa (v. KENNEL, Fig. 80, *am*). The margins of the cap-shaped embryo now become approximated and fuse together, so that the embryo becomes a closed vesicle. The embryo then grows out from the wall into the cavity of the uterus; its point of attachment narrows and thus forms a stalk (Fig. 80, *n*). A proliferation of cells then takes place at the base of the stalk, this growth being called by v. KENNEL the "embryonic placenta." Corresponding to this is a

FIG. 80.—Median section of a pear-shaped embryo of *P. Edwardsii*, with amnion and uterine wall (after J. v. KENNEL). *am*, amnion; *n*, umbilical cord; *p.e*, embryonic, *p.u*, uterine placenta; *Ue*, uterine epithelium; *Uw*, wall of the uterus; *w*, point of ingrowth.

circular thickening of the uterine epithelium, which, as the "uterine placenta," enters into close connection with the former (Fig. 80, *p.e* and *p.u*). The stalk connecting the embryo with the placenta continues to narrow, and is described by v. Kennel as the "umbilical cord." According to this account the embryo becomes closely connected with the wall of the uterus, and a thickening of the connective tissue layer of the latter takes place, causing a constriction of the uterine lumen in front of and behind the region which contains the embryo, thus forming a closed brood-cavity (Fig. 88, p. 179). The amnion and the uterine epithelium are now separated from the embryo by a considerable cavity (Fig. 80).

The germ-layers begin to form by an active increase and a consequent ingrowth of the cells which commences opposite the point of attachment of the embryo (Fig. 80, *w*). In comparing the development of *P. Edwardsii* with that of other species of *Peripatus*, the point at which this ingrowth takes place will recall the accumulation of cells in the blastoderm in *P. novae-zealandiae*, in which invagination eventually occurs, and which at the same time represents the first indications of the germ-band. In the South American species this point of ingrowth, which in position corresponds to the ventral side of the embryo (the latter is attached by its dorsal surface), must be regarded as the blastopore. From this point the ingrowth proceeds continuously, and fills the whole inner space of the embryo down to the "umbilical cord" (Fig. 80). The cells of the latter have shifted apart, leaving a central lumen, and have become arranged into an epithelium such as is also found all round the embryo, except at the point of ingrowth (Fig. 81). This outer epithelium corresponds to the ectoderm. The further differentiation of the germ-layers is said by v. Kennel to take place through the appearance of a cavity in the more dorsal part of the central cell-mass and the regular arrangement of the cells in its neighbourhood (Fig. 81, *ent*). The cell-layer thus differentiated, the entoderm, is in this way distinguished from the ventral cell-mass lying at the blastopore, which represents the mesoderm. This latter remains connected with the ectoderm for a long time, even during the later changes of shape of the embryo, and at this point (*w*) new cell-material is continually produced (v. Kennel, Sclater).

In the above description of the first ontogenetic processes in *P. Edwardsii*, we have followed the account given by v. Kennel because the material at his disposal, with regard to quantity and state of preservation, seems to guarantee the reliability of his statements, but it should be mentioned that these processes have received another interpretation. Although this latter has been opposed by v. Kennel for very important reasons (No. 5), it has been adopted by Sclater, and seems to have a certain value in so far as it affords some explanation of the peculiar early developmental stages.

According to Sclater (No. 9), cleavage gives rise to a blastula formed of large cells, and containing a small cavity (Fig. 82 *A*). An invagination then takes place in this (pseudogastrula, Fig. 82 *B*). The invaginated part alone yields the embryo (Sclater), while the outer layer, by the peculiar growth of its cells, separates from the embryo and becomes very thin, thus forming a membrane which envelops the embryo (Fig. 82 *C*, *a*). From the embryo itself another envelope arises, by the splitting off of single cells, this latter corresponding to the amnion described by v. Kennel.

Fig. 81.—Median section through a pear-shaped embryo of *P. Edwardsii* (after v. Kennel). *ent*, entoderm; *n*, umbilical cord; *w*, point of growth.

The figures given by Sclater agree on the whole with those of v. Kennel, but they are interpreted by the two authors in an entirely different way. What v. Kennel regards as uterine epithelium is considered by Sclater as an embryonic envelope, for this no doubt is the meaning of his pseudogastrula. Fig. 79 *B* (v. Kennel) must therefore be regarded as the stage of invagination corresponding to Fig. 82 *B* (Sclater's pseudogastrula), and Fig. 80 must be interpreted in a similar way. Fig. 79 *A*, according to this view, should be regarded as an older stage, similar to that represented in Fig. 82 *C*. Further, the two stages in which the conjectural vesicle has either thin or thicker walls ought not to be unhesitatingly derived one from the other, as is done by Sclater. Indeed, far stronger proofs must be brought forward for the view adopted by Sclater before it can be finally accepted; it nevertheless appears to us worth mentioning because it seems best to account for the origin of the embryonic envelopes which are attributed to *Peripatus*.* In any case, the two envelopes which are said to surround the embryo suggest the double embryonic envelopes (amnion and serosa) of the Insecta, all the more that this double embryonic integument may have arisen here as there by the formation of folds in the blastoderm. The position of the embryo in relation to the folds might even correspond to that of the Insectan germ in relation to the embryonic integuments, but we know too little of the

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* [Willey's observations on the development of *P. novae-britanniae* (App. to Lit. on Onychophora, No. II.), in which he finds that the egg gives rise to a large, thin-walled vesicle (trophoblast) with a thickened invaginated embryonic area, tend to support Sclater's views regarding the relations of embryonic envelopes in *P. Edwardsii*, and are opposed to those of v. Kennel. To us they appear conclusive on this point.—Ed.]

ontogeny of *Peripatus* to be able to make further comparisons. We must, however, add the description given by L. SHELDON (No. 12) of the earlier stages of *P. novae-zealandiae*, according to which the embryo proper still within the egg-shell is surrounded by a layer of yolk (the ectodermal yolk of Miss SHELDON). Unfortunately no details as to the significance and origin of this "external yolk" are known, but we might in this also see an embryonic envelope, especially as structures resembling nuclei are found in this outer layer. We are led to adopt this assumption all the more on account of the condition of those Insecta (or Myriopoda) in which the germ-band sinks into the yolk, a condition which finally leads to formation of the embryonic envelopes. In consequence of the Insectan embryonic envelopes arising in this way the embryo here also may be apparently surrounded by an outer layer of yolk, which in reality lies between the embryonic envelopes.

The presence of such envelopes derived from folds is not confirmed by what is found in *P. capensis*. In this form nothing of the kind has been observed, nor can we assume that such a feature has been overlooked. The ectoderm of *P. capensis* is only so far peculiar in that it is in the younger stage extraordinarily rich in vacuoles and of a spongy texture, and, in consequence of its structure, is able to take in nourishment endosmotically (SEDGWICK, No. 10). L. SHELDON connects this structure with the so-called ectodermal yolk of the New Zealand species, but we cannot consider this a happy comparison. On the other hand, this condition of the ectoderm helps to explain the formation of the external organs of nutrition in the embryos of the American species, whether these are formed direct from the ectoderm of the embryo itself or represent a specially differentiated portion of the embryonic envelopes.

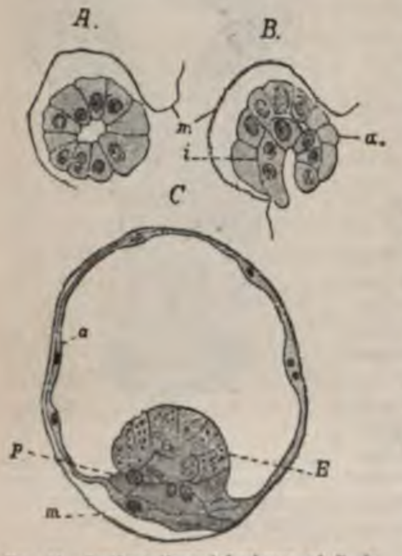

FIG. 82.—Sections through embryos of *P. Imthurni* at various stages (after SCLATER). *E*, embryo; *a*, outer, *i*, inner cell-layer of the embryo; *m*, (cuticular) membrane bounding the uterus internally; *p*, placenta-like growth of cells.

If, in dealing with the early ontogeny of the different species of *Peripatus*, we have appeared to dwell almost entirely on the relative probabilities of the processes described, we can only again point out how very little is known with certainty of the earliest development of this animal. The great importance of this form forces us to take into account statements that are not sufficiently confirmed. We have therefore tried to gather together the facts as yet known into a connected whole, but do not for one moment assume that the conclusions arrived at are final.

2. The Development of the External Form of the Body.

In spite of the variations found in the first ontogenetic stages of the several species of *Peripatus*, the latter differ very little from one another in the development of the external form of the body. In the following descriptions we shall first deal chiefly with *P. capensis*, which was very carefully examined first by MOSELEY (No. 6), then by BALFOUR (No. 1), and later by SEDGWICK (No. 10, Pt. i.).

P. capensis. It has already been shown, in describing the formation of the germ-bands, that a thickening of the blastoderm arises behind the lengthening blastopore by the proliferation of cells, this spot being recognisable externally as an oval area (Fig. 83). We saw that at this point the mesoderm originates, and extends forwards in the form of two bands, to the right and left of the blastopore. In each mesoderm-band segmentation takes place, a segmentation which may in all respects be compared to that of the Annelida. For instance, at the anterior ends of the two bands, cell-complexes are cut off and commence, by the formation of cavities, to form the primitive segments (Fig. 84 *A* and *B*), fresh rudiments being continually added posteriorly. At the posterior end of the blastopore the mesoderm-bands pass over into an undifferentiated cell-mass.

During the differentiation of the mesoderm-bands another important change takes place in the embryo. The lips in the middle region of the elongated blastopore approach one another and fuse, so that the only remains of the blastopore are an anterior and a posterior aperture (Fig. 84 *A* and *B*). These two apertures are henceforward retained (*C* and *D*), giving origin (in connection with ectodermal invaginations) to the mouth and the anus.

The next changes in the embryo take place as follows: as the differentiation of the primitive segments continues, the first of these shift further forward, and, in addition to this internal segmentation of the embryo, an outer segmentation now appears (Fig. 84). At the anterior end the cephalic lobes begin to appear, and it is to be specially noted that, as rudiments, they show great resemblance to the body-segments. The posterior end of the hitherto straight embryo curves round

FIG. 83.—Embryo of *P. capensis* (after BALFOUR). *bl*, blastopore; *w*, zone of growth.

ventrally, thus covering the posterior aperture derived from the constriction of the blastopore (Figs. 84 and 85).

Before describing the further development of the embryo, we must glance at the corresponding processes in other species of *Peripatus*. The observations recorded above on the development of the external form have dealt chiefly with the shaping of the ventral surface, this being first developed as two symmetrical halves. We are here reminded of the development of the eggs of the Oligochaeta and Hirudinea that are rich in yolk, and still more of that of the eggs of the Myriopoda, Insecta, and Arachnida. In *Peripatus*, as in these, a germ-band forms. Its composition out of two halves is still more distinct in *P. novae-zealandiae*. In this form, in consequence of the large size of the egg, caused by the abundance of its yolk, the two halves of the germ-band lie somewhat far apart, separated by a ventral protrusion of the yolk-mass covered with ectoderm and entoderm (Fig. 86 *A* and *B*), so that a kind of ventral yolk-sac arises resembling the one met with in the Araneae (p. 54). While already well developed at the anterior end, the two halves of the germ-band become less and less differentiated posteriorly, and end near the blastopore in the as yet undifferentiated cell-mass (primitive streak of English authors).

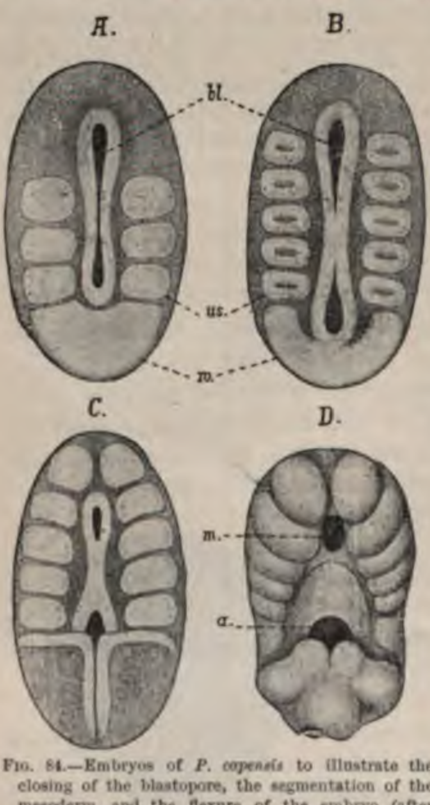

FIG. 84.—Embryos of *P. capensis* to illustrate the closing of the blastopore, the segmentation of the mesoderm, and the flexure of the embryo (after BALFOUR and SCHIMKEWITSCH). *a*, anus; *bl*, blastopore; *m*, mouth; *us*, primitive segments; *w*, zone of growth.

At first sight there appears to be a fundamental difference between *P. capensis* with *P. Edwardsii* and *P. novae-zealandiae* regarding the position, relative to the anus (?=blastopore), of this undifferentiated cell-mass (primitive streak). In the two first species this zone of growth is undoubtedly situated behind the anus (*i.e.*, behind the blastopore=anus in *P. capensis*, Fig. 84 *A*, *w*, and in the region of the blastopore and behind the anus in *P. Edwardsii*, Fig. 89 *A*), whereas in *P. novae-zealandiae* this zone of growth appears, from a superficial examination, to be situated in front of the anus (Fig. 86 *A*), at least the two halves of the germ-band bend forward and unite in front of that aperture. According to L. SHELDON this is only an apparent difference, for in sections of *P. novae-zealandiae* through this region the zone of growth of the mesoderm (primitive streak) is found to be situated, as in *P. capensis* and *P. Edwardsii*, behind, not in front of, the anus. The possibility of the zone of growth being situated in front of the anus is of interest when we make a comparison between the embryos of *Peripatus* at this stage and those of the Annelida. Such a comparison made between the embryo of *P. novae-zealandiae* (Fig. 86 *A*) and that of *Clepsine* among the Hirudinea (Vol. i., Fig. 152, p. 322) reveals a striking similarity between the two, especially in the configuration of the mesoderm-bands which, in the Hirudinea, however, unite in front of the anus, a condition which, it is true, is suggested from a superficial examination of the embryo of *P. novae-zealandiae*, but which is not substantiated by the investigation of sections, and one which would, moreover, seem improbable from a comparison with the two other species of *Peripatus* mentioned above. Further, in the Hirudinea, there appears to be no connection between the blastopore and the anus, which makes a comparison with *Peripatus* more difficult than would otherwise be the case. In other Annelida, however, the primitive mesoderm-cells are met with at the posterior edge of the blastopore (Vol. i., pp. 264 and 283), but the condition is different from that in *Peripatus* in so far as the blastopore does not pass direct into the anus. In view of these possible differences between the species of *Peripatus inter se* and of the possible resemblances to some Hirudinea, a renewed investigation of the relations of the growing zone in *P. novae-zealandiae*, which must be regarded as the most primitive form [one of the most specialised according to WILLEY and v. KENNEL], is much to be desired.

FIG. 85.—Embryo of *P. capensis* (after BALFOUR and SEDGWICK). *a*, anus; *m*, mouth.

The **South American species,** in consequence of the small size of their eggs and of the connection of the latter with the wall of the uterus, have a different form in the early stages. Our description of the embryo ceased at a stage in which it was somewhat pear-shaped (Figs. 80 and 81). From this stage it passes into the mushroom stage (Fig. 87), the embryo proper gaining in size as compared with the umbilical cord, through extending in both directions at right angles to the axis of the cord (Fig. 87). These two directions correspond to the length and the breadth of the embryo. Growth takes place at first chiefly in the first of these two directions, with the result that the embryo becomes elongate (Fig. 88). Dorsally, it is attached by the umbilical cord, while the ventral surface is free. The blunt end becomes the head, and the pointed end the posterior extremity. The blastopore, which is probably secondarily displaced, lies quite near the latter (Fig. 89 *A*, *bl*). The space between the blastopore and the umbilical cord is much longer than that between the latter and the anterior end, since, starting from the blastopore, new cell-material is continually being produced posteriorly. Two mesoderm-bands, divided up into the primitive segments, are present as in *P. capensis*, but, in consequence of the smaller size of the egg, the paired nature of the germ-band is not so distinct, although it can be recognised here also (Fig. 89).

The mouth arises in a position corresponding to that in *P. capensis*, but quite independent of the blastopore, the latter, as a small and shallow depression, having come to lie at an early stage at the posterior end (Fig. 89 *A*, *bl*). The anus also is said by v. Kennel to arise independently of the blastopore. It arises in front of the latter as a slit-like depression (Fig. 89 *A*, *a*).

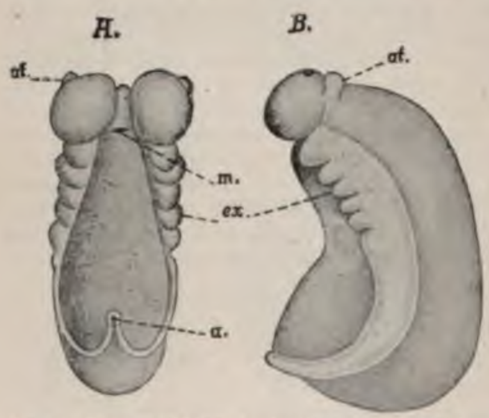

Fig. 86.—Embryos of *P. novae-zealandiae*. *A*, ventral, and *B*, lateral aspect (after L. Sheldon). *a*, anus; *at*, antennae; *ex*, limbs; *m*, mouth.

If the accounts given of *P. capensis* by Sedgwick prove correct, we shall have to conclude that, in *P. Edwardsii* also, the oral and anal apertures were originally connected with the blastopore, since the position of the two apertures is similar to that in *P. capensis*.

With regard to the position of the growing zone, *P. Edwardsii*, according to v. Kennel, agrees entirely with *P. capensis* and *P. novae-zealandiae*; for since this zone proceeds from the blastopore, and the latter lies behind the anus (Fig. 89 *A*), the undifferentiated cell-mass is also found behind it.

The connection of the embryo with the mother must here again be referred to. According to v. Kennel, the embryo is connected with the mother by means of the umbilical cord, as well as by the embryonic and uterine placenta (Fig. 80, p. 171, and Figs. 87–89). The great development of these organs shows that, in the younger stages, they contribute to its nourishment. They degenerate later, and the embryo is then, like that of *P. capensis*, nourished by the uterine secretion. In consequence of the close organic connection of the embryo with the uterus, the former is unable to shift from its position. The embryo, firmly enclosed in its brood-sac (Fig. 88), can only move on into the vagina by the growth of the parts lying between the ovary and the brood-cavity itself, and by the gradual absorption of the posterior parts. When the embryo which lies nearest the vagina passes over into the latter, its brood-cavity must be completely absorbed before the next embryo can reach the vagina.

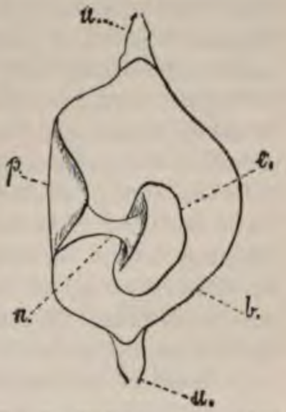

FIG. 87.—Mushroom-shaped embryo of *P. Edwardsii* in the brood-cavity (after v. KENNEL). *b*, brood-cavity; *e*, embryo; *n*, umbilical cord; *p*, placenta; *u*, lumen of the uterus.

The extrusion of the embryos in the South American species of *Peripatus* closely resembles the passage of Insectan eggs from the oviduct into the efferent apparatus. There also the empty follicle left after the expulsion of the egg is completely absorbed before the next egg is able to pass out.

The further development of the external form of the body consists essentially in the lengthening of the body, the marking off of the head and trunk, and the appearance of the limbs and sensory organs. It agrees on the whole in the different species, so that separate accounts are here unnecessary.

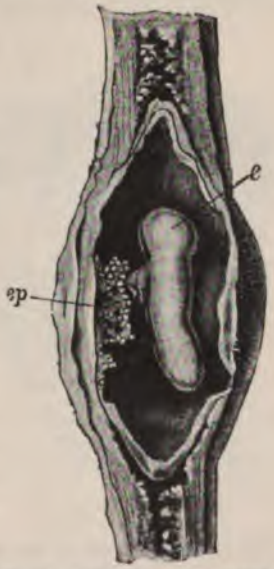

FIG. 88.—Embryo of *P. Edwardsii* in the brood-cavity (after J. v. KENNEL, from LANG'S *Text-book of Comp. Anat.*). *e*, embryo; *ep*, placenta.

An important change in the form of the young embryo is brought about by the great development and marking off of the cephalic segment from the trunk (Figs. 86 and 89). This change, which occurs early, is introduced by the shifting forward of the first pair of primitive segments to the extreme anterior end of the body, where they become considerably enlarged. A pair of large swellings (cephalic lobes) thus arise at the anterior end; these soon become marked off from the body by a transverse furrow, and thus constitute the cephalic segment. On the ventral side of these lobes is the oral aperture; on the dorsal side a pair of prominences appear (Fig. 86 *A* and *B*) which soon increase in size and become recognisable as the rudiments of the antennae. In *P. capensis* these are said to appear before the limbs (Sedgwick), but this distinction seems to be of no great significance; in *P. Edwardsii* the antennae are said to appear simultaneously with the rudiments of the truncated legs, which they closely resemble. They are, however, distinguished from the latter by their more dorsal and pre-oral position (Figs. 86, 90, and 91).

In front of the rudiments of the antennae, and lying more medianly, there are, at an earlier stage, two small prominences (Fig. 90, *x*), which shift later towards the anterior margin of the head (Fig. 94 *A* and *B*). These prominences, which were observed by v. Kennel in *P. Edwardsii*, and the nature of which is as yet unknown, can still be recognised at a later stage than that depicted in Fig. 94 *B*, and disappear from view only when folds begin to form in the cephalic integument. We shall refer to them again at the end of this section (p. 187).

Fig. 89.—Embryo of *P. Edwardsii*. *A*, ventral, and *B*, lateral aspect (after v. Kennel). *a*, anus; *bl*, blastopore; *m*, mouth; *n*, umbilical cord.

The limbs arise as latero-ventral outgrowths of the segments consecutively from before backward (Figs. 86, 90, and 91). The segmentation of the body is brought about chiefly by the outgrowth laterally of the primitive segments. The embryo, especially in its lateral parts, thus appears notched (Figs. 86 and 90). The paired nature of the germ-band is still indicated by the presence of a median ventral furrow (Fig. 89). This especially applies to *P. Edwardsii*, in which also the limbs appear later than in the African and Australian species. This retardation is no doubt due to the modified method of development within the uterus, the close connection of the embryo with the wall of the uterus leading to the later development of its external form. In *P. novae-zealandiae* the limbs are to be found while the two halves of the germ-band are still far apart (Fig. 86), and in *P. capensis* also they appear early.

The embryo, at an early stage, becomes curved, and, as the body elongates, its posterior end becomes rolled up ventrally (Fig. 85, p. 177), this being determined either by its position within the egg-shell or (secondarily as in *P. Edwardsii*) within the brood-cavity. In *P. Edwardsii* the posterior end forms several coils. The posterior extremity of the embryo of *P. capensis* is also at first bent in towards the ventral surface of the body (Fig. 85), but subsequently this posterior region grows parallel with that surface, the bend being retained at the middle of the body, and the embryo lies in the egg-envelope in such a way that the anterior and posterior halves of the body are almost parallel to one another, the head touching the posterior end.

In *P. novae-zealandiae*, in a stage earlier than that illustrated in Fig. 86 *A* and *B*, a ventral flexion apparently occurs in the embryo, the latter consequently assuming a curved form, but it soon straightens again to some extent, and retains the form shown in Fig. 86 *A* and *B* (L. SHELDON, No. 12, Pt. i.). Here also the two halves of the germ-band are at first very far apart, as may be seen from Fig. 86 *A* and *B*.

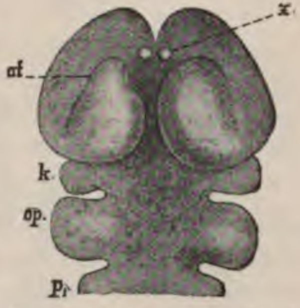

FIG. 90.—Anterior part of an embryo of *P. Edwardsii*, dorsal aspect (after v. KENNEL). *at*, antenna; *k*, maxillary segment; *op*, segment of the oral papillae; *p*, first adult trunk segment; *x*, prominence in front of the antennal rudiment (*cf.* pp. 180 and 187).

In keeping with the unspecialised external form of the adult *Peripatus*, the further development of the embryo is very simple, and, apart from the anterior region of the body, presents no specially noteworthy features. The formation of the limbs continues in the manner above described (Fig. 91), until the final number is reached. Where the two halves of the germ-band lie far apart, as in *P. novae-zealandiae*, they eventually shift together to form the ventral surface, a process which is assisted by the gradual absorption of the yolk. The dorsal surface at the same time assumes its final shape. The annulations of the body, and the papillae which are seen on its surface in the adult condition, appear in the form of folds and slight elevations of the epidermis.

The terminal region of the body, up to the time when the adult form is assumed, is almost button-shaped. At its lower side, either in a depression (as in *P. Edwardsii*) or on a papilla, as in *P. capensis*, lies the anus. Two slight outgrowths, the anal papillae, which apparently belong to the terminal section, must be regarded as rudiments of limbs, and thus indicate a true segment. The limbs themselves have assumed their adult form, being better marked off from the body, and exhibiting a ringed appearance not unlike segmentation At their free ends the two cuticular chitinous claws arise. The limbs have shifted from their former more ventral position to their final position between the dorsal and the ventral surface.

With regard to the position of the anus it must be mentioned further that, in consequence of its being found in front of the growing zone, it must be related to a true segment. In various drawings made by v. KENNEL and SEDGWICK of sections cut through the anal aperture, well developed primitive segments are seen round the terminal region of the intestine. We must then in any case assume a shifting forward of the anus which originally belonged to the terminal region of the body. The relation of the anus to the segmentation of the body in the adult does not seem satisfactorily settled, nor is it clear whether it subsequently shifts out of the segmented region to the extreme end.

The development of the anterior region of the body is less simple than that of the trunk. Complications arise in the former through two other segments besides the actual cephalic segment being drawn into the formation of the adult head, and through the corresponding modification of the appendages of these segments. We thus find in *Peripatus* a state of things already met with in the Crustacea, and still more closely resembling conditions found in the Arachnida, Myriopoda, and Insecta.

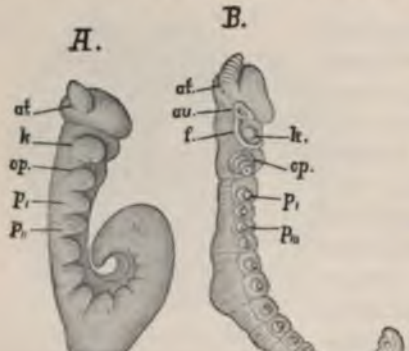

FIG. 91.—Embryos of *P. capensis* of different ages (after SEDGWICK). *at*, antenna; *au*, eye; *f*, fold, contributing to the formation of the buccal cavity; *k*, jaw; *op*, oral papilla; p_{I}-p_{III}, first three pairs of limbs.

In the cephalic segment, the rudiments of the antennae have undergone alteration; they have lengthened considerably, and rings like those on the limbs have appeared on them (Fig. 91, *at*). The eyes (*au*), as slight ectodermal depressions, are already present as rudiments (*P. capensis*), situated somewhat ventrally to the antennae. In *P. Edwardsii* they arise immediately behind the bases of the antennae.

The further development of the mouth and of the two pairs of limbs connected with it is of special importance. The anterior aperture remaining after the partial closing of the blastopore does not directly give rise to the mouth, but becomes carried inwards by an invagination of the ectoderm, the stomodaeum, and thus forms the aperture between the latter and the enteron.* Neither does this second aperture represent the mouth of the adult, for it becomes covered by various outgrowths of the ectoderm, which form above it a secondary buccal cavity. This process commences by the appearance of a fold on the outer side of the limb next in order to the antenna (Figs. 91 and 92, *k*); this fold is closely applied to the limb, and is continued posteriorly along the ventral surface of the embryo (Figs. 91 and 93, *f*, and Fig. 92, *p*). It appears notched, and, in *P. Edwardsii*, is represented by a series of papillae lying one close to the other (Figs. 92 and 94). In later stages these two folds shift closer towards the oral aperture, and thus press the limb-rudiments that lie on the inner side of them towards the mouth. As the folds grow still higher, these limbs, together with the stomodaeal aperture, come to lie in a cavity, the adult buccal cavity (Fig. 94), the limbs themselves becoming the jaws of the adult. The distal part of each of the limbs, at the time when the formation of the buccal cavity just described begins, appears deeply notched, and the two strong chitinous teeth arise at this part (Fig. 94 *A* and *B*). These terminal teeth, which are to be compared with the double claws on each of the legs, prove, even in the adult, that these jaws are true limbs.

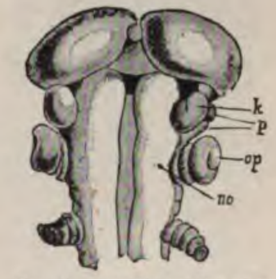

FIG. 92.– Anterior portion of an embryo of *P. Edwardsii*, seen from the ventral side (after v. KENNEL, from LANG'S *Text-book of Comp. Anat.*). *k*, jaw; *no*, aperture of the nephridium belonging to the segment of the oral papillae (*op*); *p*, papillae of the folds which surround the jaws laterally.

Several other structures contribute to the complete development of the buccal cavity. Between the cephalic lobes, and ventrally to them, a somewhat long prominence arises (Fig. 94, *ol*), which

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* *Cf.* below, p. 196.

lies directly in front of the sharp edge of the stomodaeal aperture, and thus, when that aperture is walled in by the lateral folds, shifts with it into the cavity thus formed (Fig. 94 *B*). The folds then unite in front of this unpaired papilla, the upper lip of v. KENNEL (Fig. 95). The posterior unnotched continuations of the lateral folds form the posterior boundary of the buccal cavity, on the floor of which the primitive aperture of the stomodaeum now lies surrounded by the jaws and the upper lip.

From the above it will be seen that, in *Peripatus*, there are three distinct apertures, each of which in turn must be regarded as the oral aperture: (1) the primitive blastoporic mouth (Fig. 84 *D*, *m*), which persists in the adult as the opening between the oesophagus and the stomach-intestine; (2) the stomodaeal mouth (Fig. 93, *m*), which in the adult puts the buccal cavity into communication with the pharynx; and (3) the external opening of the buccal cavity, which functions as the mouth in the adult, and is formed by the concrescence of two ectodermal folds.

FIG. 93.—Cephalic part of an embryo of *P. capensis* (after SEDGWICK). *at*, antenna; *f*, oral fold; *k*, jaw; *m*, stomodaeal aperture; *op*, oral papillae; *sp*, aperture of the salivary gland; *vo*, aperture of the ventral organ.

The shifting forward of the lateral folds towards the oral aperture has also caused the ventral organs of the first two segments to shift into the buccal cavity (Fig. 94 *A*, vo_1 and vo_2). We shall refer to these again later. Another pair of folds exactly like those which have walled in the oral aperture are sometimes present, according to v. KENNEL, on the outer side of the lateral folds, but these do not seem to be of constant occurrence. They, however, seem further to support the view, which appears very probable, that the folds found near the mouth of *Peripatus* do not represent limb-rudiments, as has been conjectured by MOSELEY.

The third pair of limbs are less closely connected with the mouth than are the jaws, for while they also shift towards the oral aperture, they remain outside the lips of the buccal cavity (Fig. 95, *op*). Apart from the fact that no chitinous hooks develop on them, they retain to a greater degree the character of limbs. They are early distinguished from the other limbs by their greater development (Fig. 91 *B*, *op*). These limbs are known as the oral papillae, at the tips of which the slime-glands open. In the adult, these papillae lie as far forward as the jaws (Fig. 95), and the segment to which they belong must therefore be reckoned as a cephalic segment. Three segments beside the primary cephalic segment, viz., those of the antennae, of the jaws, and of the oral papillae thus take part in the formation of the head.

The head of the embryo, in consequence of the great development of the cephalic lobes, at first appears very large in proportion to the rest of the body (Figs. 86 and 89). In the course of development, however, it decreases in size, the mouth shifts more to its anterior end, and the form of the adult is thus practically attained.

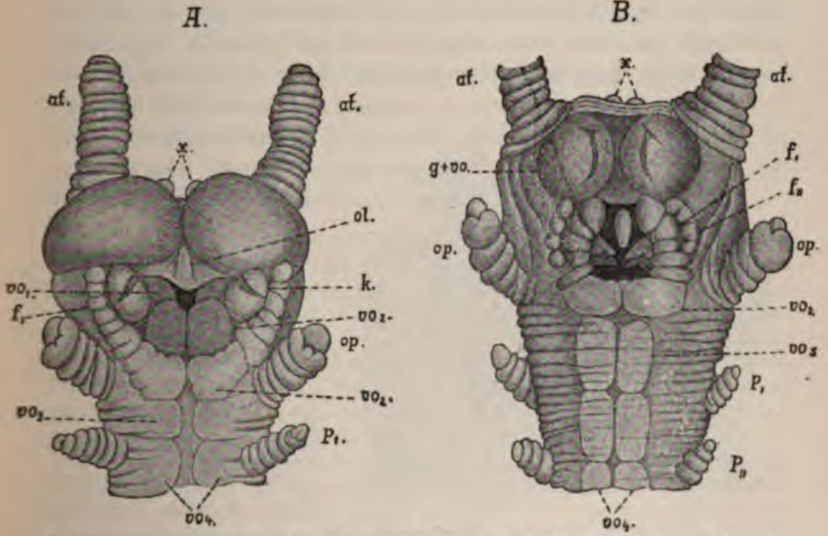

FIG. 94.—Anterior parts of embryos of *P. Edwardsii*, ventral aspect (after v. KENNEL). *at*, antenna; f_1, the folds broken up into papillae, surrounding the mouth; f_{11}, the folds lying outside of f_1; $g+vo$, ganglion and ventral organ of the cephalic segment with the slit-like depression of the ventral organ; *k*, jaws; *ol*, upper lip; *op*, oral papillae; p_1, p_{11}, first and second pairs of legs; vo_1-vo_4, ventral organs of the jaws, oral papillae, and of the first two trunk-segments; vo_2 is divided into an anterior and a posterior part; *x*, prominences in front of the antennal rudiments (pp. 180 and 187).

The young are born provided with the complete number of limbs. Their development, according to authors, lasts unusually long (SEDGWICK, No. 11). *P. novae-zealandiae* is said to require eight to nine months for its development, and *P. capensis* thirteen months (?). The umbilical cord, which in the South American species connects the embryo with the placenta, at the time when the embryo lengthens and coils up its posterior end, changes and finally degenerates; its lumen closes first near the embryo. The embryo is now nourished by swallowing the surrounding albumen, a method of feeding which also occurs in the embryos of *P. capensis*; in addition to this there is a kind of endosmotic inception of nutritive fluid.

Interpretation of the cephalic appendages of Peripatus. The nature of the two posterior pairs of cephalic appendages of *Peripatus* cannot be doubted. They correspond to the limbs of the trunk, and might without further question be assumed to be limbs which, when two (primary) trunk-segments were fused with the head, were transformed into jaws and oral papillae. This is not the case with the antennae, which are distinguished from the limbs of the trunk by their dorsal and pre-oral position. In this respect they entirely agree with the antennae of the Myriopoda and the Insecta, with which we consider them homologous. The antennae of *Peripatus* seem undoubtedly homologous with those of all the other Tracheata, but not with those of the Annelida. The antennae, not only of *Peripatus*, but of the Myriopoda and Insecta, have been compared with regard to their position to the cephalic tentacles of the Annelida, which are found (pre-orally) in the cephalic segment, occupying the same position with relation to the neural plate as do the antennae of the higher forms with relation to the brain. The manner in which the antennae of *Peripatus* originate, however, seems to us to tell against such a comparison. The antennae, both as rudiments and when developing, show great agreement with the trunk-limbs (Figs. 91–94), a fact which is strikingly evident in the figures given by SEDGWICK and v. KENNEL. Like the limbs, they are externally ringed, and a process of the primitive segment runs into each of them, so that they too are hollow cones. Indeed, a canal is said to run from the primitive segment of the antenna

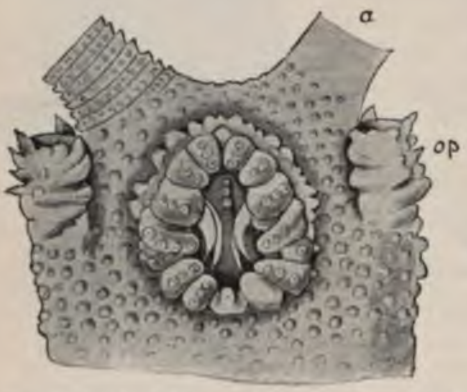

Fig. 95.—Head of *P. Edwardsii*, ventral aspect (after SEDGWICK, from LANG's *Text-book of Comp. Anat.*). *a*, antenna (the greater part of which is removed); *op*, oral papilla. In the buccal cavity are the double jaws. The cavity itself is surrounded by the folds cut up into papillae.

to the exterior, and this would correspond to the nephridial canal of the trunk-segments. In fact, there is such close agreement between the antennae and limbs as rudiments, that it is difficult to believe that they are essentially different structures. We should feel inclined rather to attribute to them the same origin, and to assume merely that the antennae had shifted further forward. This conjecture is supported by a comparison of the antennae of the Insecta with those of *Peripatus*. The former also as rudiments show not only in form, which would there be less remarkable, but also in position the closest agreement with the (primary) trunk-appendages, indeed, to begin with they even lie post-orally (Fig. 147). We might conclude from this that the antennae of *Peripatus* and those of the Insecta were homologous structures, but that they could not be compared with the cephalic tentacles of the Annelida, in other words, that they were originally appendages of the primary trunk and not of the primary cephalic region.

If we accept this view we shall have to assume that the primary cephalic region has greatly degenerated, and that a primary trunk-segment (the first) has to a certain extent taken its place. An indication as to how and why this happened is to be looked for in the fusion of the other and undoubted trunk-segments in the adult head. The utilisation of the anterior limbs as mouth-parts was accompanied by their partial transformation into sensory organs (palps of the Insecta), and the final preponderance of one pair as feelers. Again the brain would in this case have to be reckoned as belonging to the first (primary) trunk-segment, and could not be derived from the neural plate alone. This view, however, presents no difficulty when we see how, in *Peripatus*, the ganglia of the maxillary segment passes from a post-oral to a pre-oral position and is absorbed into the brain (p. 193). In the Crustacea the ganglia of the second antennae undergo corresponding changes.

The entire filling up of the so-called cephalic segment in *Peripatus* by a regular pair of primitive segments with unbroken epithelial walls agrees with what is found in a trunk-segment, but not with the condition of the cephalic region in the Annelida.

If the primary cephalic segment which, in the Annelidan *Trochophore*, carries the cephalic tentacles, has really undergone degeneration, we might expect to find traces of this fact. The two small prominences which appear in front of the antennal rudiments, the significance of which is still obscure, might be regarded as vestiges of this kind (Figs. 90 and 94, *x*). We might conjecture that they are possibly *vestiges of the primary Annelidan tentacles*. This interpretation of them, which appears to us very plausible, also leads to a striking agreement with the Crustacea. In homologising the cephalic appendages of the latter (Vol. ii., p. 166), a similar view was adopted, the same significance being ascribed to the frontal sensory organs as is now given to the small prominences (*x*) in front of the antennal rudiments in *Peripatus*.

It cannot be regarded as altogether improbable that the adult *Peripatus* should still retain vestiges of this organ, the agreement of which with the frontal sensory organs still functioning in many Crustacean larvae would be stil more striking. The prominences now under consideration are, according to v. KENNEL, retained for a long time, and have perhaps escaped observation in later stages owing to the development of papilla-like prominences of the integument, such as occur in great numbers in the adult. ST. REMY (No. 8) describes and illustrates a paired ganglionic swelling on the brain of the adult *Peripatus* ("formation de nature inconnue"), which in position corresponds to the two prominences on the head of the embryo, and which might well be regarded as the lobe of a primary tentacle-nerve. In the posthumous works of BALFOUR also, similar structures are described as pairs of nerves (running to various points of the dorsal surface), and of these one might belong to such a sensory organ.

We cannot refrain, in this connection, from calling attention to the sensory organs found in the cephalic region in many Myriopoda (*e.g.*, *Lithobius*, *Polyxenus*, and *Glomeris*), the innervation of which is said to take place from the "optic thalamus" (TOMOSVARY, No. 22, p. 760). We must however impress upon the reader that the actual material required for a successful comparison of this peculiar sensory organ with the frontal organ of the Crustacea, or with the still insufficiently investigated prominences of *Peripatus* has not yet been obtained.

In the younger embryos of *Peripatus* (such as that illustrated in Fig. 91 *A*), the change of position of the antennae, if these are considered as proceeding from limbs, is not very marked, especially as compared with the corresponding change that takes place in the Insecta. The position of the eyes in *Peripatus* is less easily reconciled with this view. The eyes lie further back than the antennae, close to that part of the brain which must be derived from the first (primary) trunk-segment. The eyes, however, may well be ascribed to the primary cephalic segment, especially as, in *Peripatus*, they agree with the eyes of the Annelida rather than with those of the Arthropoda. This can only be explained as having been brought about by the shifting of the various parts which participate in the formation of the head.

3. The Formation of the Organs.

The Ectodermal Structures.

The Integument.

The ectoderm forms a single layer of cubical cells over the greater part of the body of the embryo. In *P. capensis* these cells, especially on the dorsal surface, are said by SEDGWICK not to be sharply demarcated externally, and to exhibit a spongy structure. SEDGWICK on this account ascribes to them the capacity for absorbing fluid nourishment, and believes that the placenta described by v. KENNEL might arise as a more specialised ectodermal organ for taking in nourishment. The changes undergone by the ectoderm when transformed into the adult integument are not very important. The delicate cuticle which occurs in the adult is secreted externally. At some points, *e.g.*, on the ventral side of the limbs, the ectoderm becomes multilaminar and here secretes a thicker layer of chitin, and this is also the case at the distal extremities of the limbs where the claws are formed.

The Nervous System and the Ventral Organs.

The nervous system and the ventral organs arise from two massive thickenings of the ectoderm formed by the active increase in number of the cells on the ventral side of the cephalic and primary trunk-segments. The two longitudinal swellings thus produced appear at the time when the limbs become sharply marked off from the body, and develop from before backward.

According to SEDGWICK, each of these swellings passes directly into a corresponding thickening of the cephalic (antennal) segment, but this, according to v. KENNEL, is not the case, the swellings ending bluntly where the cephalic section commences (Fig. 92), so that the part of the central nervous system pertaining to the cephalic segment arises separately from the rest.* A much slighter thickening of the ectoderm does, however, occur, according to v. KENNEL, between the cephalic and the trunk portions of the longitudinal swellings at the time when the latter appear. And this, since it denotes the formation of a commissure, might be regarded as indicative of a continuity between the cephalic and the trunk portions of the longitudinal swellings. This question as to the continuous origin of the cephalic and the trunk portions of the central nervous system has already been discussed in connection with the Annelida (Vol. i., p. 287). It was not indeed there finally settled, but it is in connection with them that a decision of the question can best be expected.

The paired thickening on the ventral surface just described gives origin not only to the nervous system, but also to the ventral organs (v. KENNEL, No. 4). Transverse sections of the embryo show that the thickening projects both externally and internally (Figs. 100, p. 200, and 101, p. 202). In the middle of the cell-mass which forms it, a horizontal fissure then arises extending from before backwards and separating the mass into an outer and an inner portion (Fig. 100 *B*). The inner mass of cells represents the rudiment of the nervous system (*n*), the outer, remaining in connection with the epidermis, represents that of the so-called ventral organs (*vo*), the development and significance of which must now be discussed.

The ventral organs. As the cleft, which in each segment divides the rudiment of the nervous system from that of the corresponding ventral organ, is interrupted by intersegmental cellular strands connecting its two walls (Fig. 101 *B*, p. 202), a segmentation of the ventral organs takes place which is visible even externally. The connecting strands between the ventral organ and the nerve-cord, which occur between the consecutive pairs of limbs, are retained

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* An entirely distinct origin for the brain and for the ventral chain of ganglia cannot here be asserted, inasmuch as the ganglion of the maxillary segment is also drawn into the brain, as will be shown presently. On this account and also because of the relation above pointed out, of the antennae to the limbs, there is room for doubt as to the true cephalic nature of the brain in *Peripatus*.

until the embryo is mature, and are even found in the adult (v. KENNEL). As development proceeds, the ventral organs shift together and finally unite in the middle line; they become flattened and a slight depression is seen on their outer surface. Whereas at first they were very massive (Figs. 100 and 101 *B*), they now appear much smaller as compared with the size of the embryo (Fig. 102, p. 205). As the embryo develops, they become less and less conspicuous, and, in the adult, are represented merely by a small unpaired follicular depression of the epidermis situated medianly between the bases of the limbs on each segment (v. KENNEL), and until recently overlooked.

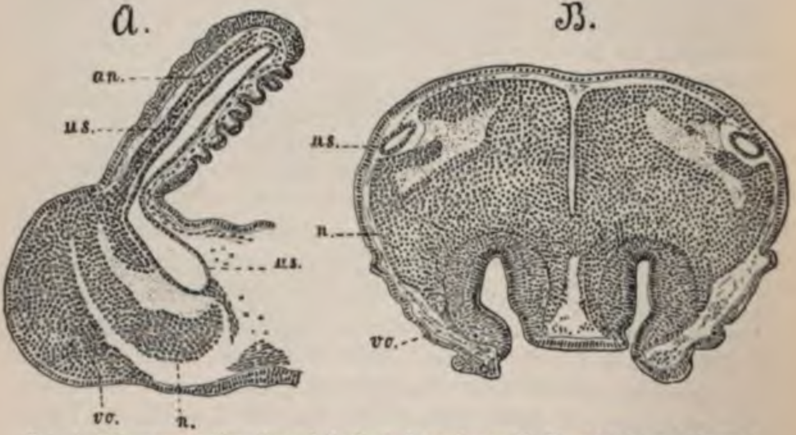

FIG. 96.—Transverse sections through the head of an embryo of *P. Edwardsii* (after v. KENNEL). In *A*, only half the section is drawn. *an*, antennal nerve; *n*, brain (consisting of cell- and fibre-substance); *us*, primitive segment of the head; *vo*, ventral organ.

The ventral organs of the anterior segments differ from the rest. Those belonging to the segment of the oral papillae, as well as those of the maxillary segment, are drawn into the buccal cavity, and can still for a time be recognised on its floor (Fig. 94 *A*, vo_1 and vo_2). Of these, the two posterior unite to form the ventral wall of the oesophagus, while the anterior organs remain distinct. Consequently each of these latter develops further independently, and in both the external depressions are more marked than the other trunk ventral organs (thus retaining, according to v. KENNEL, the more primitive character). This is still more the case with those structures which must no doubt be regarded as ventral organs of the cephalic segment. These are two deep epidermal depressions lying near one another on the ventral side of the cephalic segment (Fig. 96 *B*, *vo*), which have arisen, like the ventral organs of the trunk, by the splitting up of the ectodermal layer into an outer and an inner portion, and the subsequent invagination of the former. These depressions, which at first are quite open, but later close almost completely, can be recognised even in surface view, first as pits, and later as irregular slits on the ventral surface of the cephalic lobes (Figs. 93, p. 184, and 94 *B*, p. 185). At a later stage the ventral organs close completely and lose their connection with the epidermis. As the two vesicles sink down deep into the mass of the brain (Fig. 96 *B*) and thus become closely connected with this latter, it is clear that, when the brain becomes small in comparison to the head and shifts to the dorsal side of the latter, the vesicles follow the brain, and remain connected with it in the form of a thick-walled vesicle, the so-called brain-appendage of *Peripatus*. The ventral organ of the cephalic segment, if, indeed, this vesicle is to be considered as such, would be distinguished from those of the trunk by the complete loss of its connection with the epidermis.

The significance of the ventral organs has until now remained obscure. Their great development in the early part of embryonic life, and their reduction in the adult, indicates that they are organs which were more highly developed in the ancestors of *Peripatus*. From their position it might be concluded that perhaps the greater part of the ventral surface, by means of its strong ciliation, functioned for locomotion, like the ventral ciliated area of the Annelida. The connection of the ventral organs with the nervous system is not surprising, considering the origin of the latter out of these ectodermal masses. It is possible that during ontogeny the ventral organs may be concerned in supplying the cell-material for the development of the ventral chain of ganglia. v. KENNEL's statement that the gradually diminishing cell-mass of the ventral organs is used in the further development of the epidermis seems in keeping with the original connection of these organs with the ectoderm, especially as, with the exception of the ventral organ of the cephalic segment, the greater part of each organ retains this connection. The similarity between these cephalic ventral organs and the "cephalic pits" of the Arachnida, which are in the closest connection with the nervous system (pp. 12 and 53), is very striking. Fig. 96 *B* shows how closely the "ventral organs" of the head of *Peripatus* become applied to the rudiment of the brain, and comparison of Figs. 93 and 94 *B*, with Fig. 4 *C*, p. 6, Fig. 7, p. 10, and Fig. 28, p. 52, shows that a marked agreement exists even in the external position of the depressions in the two groups. In the present state of our knowledge, however, we are not justified in carrying this comparison further.*

The Nervous System. When the rudiments of the two longitudinal nerve-trunks first separated from those of the ventral organs,

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* [WILLEY (App. to Lit. on Onychophora, No. II.) finds what he believes to be ventral organs persisting in the adult on the anal segment.—ED.]

a thin layer of fibres had already appeared on the dorsal side of the former. As development proceeds this gradually thickens (Figs. 101, p. 202, and 102, p. 205). The position of this fibrous layer on the mass of the ganglion-cells is practically retained in the adult, for even there the fibrous mass lies dorsally to the ganglionic cells (Balfour, No. 1), and only a very few of the latter attain a position dorsally to the fibrous mass. This feature must be regarded as a primitive one. In more highly differentiated forms, *e.g.*, the Crustacea and the Arachnida, the fibrous mass is indeed peripheral when it first appears, but is soon covered by ganglionic cells, and comes to lie within the mass of the ganglion. It has already been pointed out, in connection with the Crustacea (Vol. ii., p. 162), that the appearance of the fibrous substance on the inner periphery of (*i.e.*, dorsally to) the ventral strands might represent a primitive condition.

The transverse commissures which are, in *Peripatus*, found in large numbers connecting the longitudinal nerve-trunks, grow out from the latter like the peripheral nerves, which are said to be formed by the outgrowth of nerve-fibres (v. Kennel).

The brain arises in a manner agreeing with the origin of the rest of the nervous system, but certain complications are caused by the fact that it is formed by the fusion of the ganglia of two distinct segments. The separation of the ganglionic rudiment of the cephalic segment from the epidermal thickening (ventral organ) takes place somewhat as in the trunk-segments, but the fibrous tissue here lies much deeper in the mass of ganglionic cells, and is partly covered dorsally by the latter (Fig. 96 *B*). From this dorsal cell-mass a strand of cells is continued into the antennal rudiment, and forms the rudiment of the antennal nerve (v. Kennel, No. 4, Sedgwick, No. 10, Pts. iii. and iv.). The latter therefore appears as a direct continuation of the cerebral ganglion, and is in this way distinguished from all the other peripheral nerves, which are merely outgrowths of nerve-fibres (without participation of ganglionic cells).

The nerve-mass yielded by the cephalic segment soon grows to such a size as to occupy the greater part of the head; the two masses of ganglion cells, from which the antennal nerves proceed, shift towards the middle dorsal line, where they form a pair of large egg-shaped swellings (Fig. 97, *g*). The pair of ganglia composing the brain are at first separated by a deep slit. This becomes bridged over later, the fibrous mass of the two halves of the brain uniting to form a commissure (the so-called supra-oesophageal commissure, v. KENNEL). This commissure is thus of secondary origin, and seems also to involve parts of the brain lying further back. These parts, however, do not belong to the cephalic segment, but are formed by the (maxillary) segment that follows it.

When the jaws become enclosed in the developing buccal cavity, the ganglia of the maxillary segment also sink below the surface, and pass toward the dorsal surface, so that they can soon be recognised in viewing the embryo from the dorsal side (v. KENNEL, Fig. 97, g_{III}). It must be assumed that this upward displacement takes place along the oesophageal commissures which are already present. The maxillary ganglia are thus approximated to those of the cephalic segment, with which they subsequently fuse. This fusion is very intimate, and the maxillary ganglia can be recognised as two moderate prominences behind the antennal ganglia (Fig. 97, g_{III}). The fibrous masses of the maxillary ganglia from the two sides unite to form a commissure, the sub-oesophageal commissure, this being facilitated by the downward slope of the posterior ends of these ganglia. This method of formation of the sub-oesophageal commissure renders it very improbable that it is a primitive structure. A commissure lying further back and consisting of cells (Fig. 97, *c*) might rather be considered as such. This latter commissure connects two ganglionic swellings, which may perhaps be attributed to the segment of the oral papillae. All the commissures which follow this are, as already mentioned, said to be derivatives of the fibrous substance.

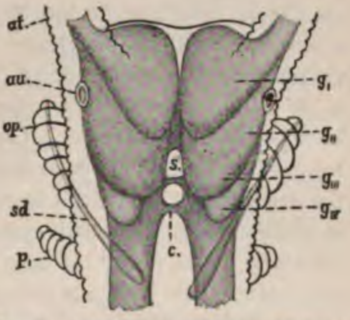

FIG. 97.—Anterior part of the central nervous system of an embryo of *P. Edwardsii* at a somewhat earlier stage than that depicted in Fig. 94 *B*, dorsal aspect (after v. KENNEL). *at*, antenna; *au*, eye; *c*, first commissure after the sub-oesophageal commissure; g_I and g_{II}, cephalic portion of the brain; g_{III}, portion belonging to the maxillary segment; g_{IV}, the next following ganglion; *op*, oral papilla; p_I, first foot; *s*, passage for the oesophagus; *sd*, slime-gland.

The point that must be regarded as of most importance in the formation of the brain in *Peripatus* is the fusion of the maxillary ganglia with the ganglia of the cephalic segment, for this feature distinguishes *Peripatus* from the Myriopoda and the Insecta so far as is at present known, and connects it rather with the Crustacea, in which the ganglia of the segment of the second antennae unite with the brain (Vol. ii., p. 165). It therefore seems likely that the jaws of *Peripatus* are to be homologised, not with the mandibles of the Insecta, but rather with the second antennae of the Crustacea. The question which naturally arises as to whether the corresponding segment has been lost in the Insecta, or, in other words, as to the relation to it of the mandibular segment, can hardly, in the present state of our knowledge, be profitably discussed.

The close connection brought about between the maxillary segment and the cephalic segment increases the probability of the view expressed above, that the antennal segment also (now known as the cephalic segment) may have been united with a cephalic section formerly present, and now to a great extent degenerated. We were led to this assumption by the presence of the two prominences in front of the antennal rudiments (Fig. 94, *x*), and by the close agreement in manner of formation between the antennae and the feet. It is, indeed, difficult to reconcile with this view the statement that the antennal nerve forms in a manner essentially different from the peripheral nerves, but this point has as yet received too little attention to be considered as of decisive importance.

The Eyes.

The rudiments of the eyes have already appeared before the separation of the nervous system from the ventral organs. On the dorsal boundary of the ectodermal thickening in the cephalic segment, a small pit is formed on each side, behind and somewhat ventrally to the rudiments of the antennae; the floor of this pit is at first connected with the ectodermal thickening, but soon becomes detached from it. The pit closes to form a vesicle, which becomes constricted off from the ectoderm. Outwardly, *i.e.*, towards the epidermis, this vesicle is unilaminar, but on the inner side it is multilaminar. Pigment appears on the inner boundaries of its cells, and in its cavity the lens is secreted. The cells of the inner and lateral walls yield the rods of the retina. A differentiation into cell- and fibre-substance has already taken place in the thickened inner wall of the optic vesicle, and a connection which occurs between this part and a process sent out by the brain gives rise to the optic nerve, which is thus a secondary formation (v. KENNEL).

SEDGWICK's account of the origin of the eyes in *Peripatus* is somewhat different. According to him, the region in which they originate still belongs to the brain, and they do not lose their connection with the latter, the inner wall of the optic vesicles remaining united with the cell-mass of the brain. The optic nerve arises at this point later by simple constriction. The eyes thus originate chiefly from the brain, and are covered merely by the ectoderm of the surface; they are "cerebral eyes," according to SEDGWICK, in opposition to v. KENNEL, who believes, as stated above, that they arise independently of the brain.

It is possible that the observations made on the origin of the eyes in *Peripatus* can be harmonised with those of the development of the eyes in the Annelida. The eyes of *Peripatus* agree closely with more highly organised Annelidan eyes, such as those of the *Alciopinae.* According to KLEINENBERG (Vol. i., p. 289, Annelidan Lit., No. 26), the eyes in this family arise independently of the cephalic ganglion as two ectodermal invaginations, but the inner wall of the optic vesicle is said to become closely connected with the brain, giving off cell-material direct to the latter. The elements of the two organs, in any case, seem for a time to be closely united, at the very point where the optic nerve forms later. If KLEINENBERG's observations are confirmed, a similar condition might be thought to prevail in *Peripatus* also, and the opposing views of v. KENNEL and SEDGWICK might thus be explained.

The Slime- and the Crural Glands.

The **slime-glands** are of ectodermal origin, arising as depressions on the tips of the oral papillae (Fig. 93). At first the pits are shallow, but they gradually deepen and their blind ends grow inwards and backwards. The pit has thus, at the stage depicted in Fig. 94 *B*, become a conical tube (Fig. 97, *sd*), which has grown back to the intestine. This growth continues in the following stages, so that the glands eventually attain a considerable length. They retain their simple tubular form; the branches which occur in them in the adult appear as outgrowths shortly before the embryo is mature and ready for birth (v. KENNEL).

The slime-glands are no doubt to be regarded as modifications of the **crural glands,** which, as sac-like structures, lie in the lateral divisions of the body-cavity and open on the ventral side of the feet. In the different species of *Peripatus* they differ in number and in distribution. These glands first appear at a late stage of embryonic development as ectodermal invaginations lying at the bases of the feet distally to the apertures of the nephridia (Fig. 102, *c*, SEDGWICK). In the male (*P. capensis*) the crural glands of the last pair of feet are transformed into long glandular tubes (BALFOUR).

The Alimentary Canal.

With the exception of the short stomodaeum and proctodaeum, which are ectodermal derivatives, the alimentary canal is of entodermal origin.

The following account is derived principally from the description given by SEDGWICK of *P. capensis*, this form being chosen because we must regard it as more primitive than the American species examined by v. KENNEL. The two forms vary principally in the first stages of the development of the intestine, the later stages showing great similarity.

In order to understand the formation of the intestine, we must revert to the gastrula stage of *P. capensis.* The blastopore there leads into a cavity, which is lined by a thick protoplasmic syncytium containing nuclei and rich in vacuoles. This voluminous nucleated mass must no doubt be regarded as corresponding to the yolk with its nuclei found in *P. novae-zealandiae.* In the latter form, the nucleated yolk forms part of the boundary of the archenteric cavity. In both forms the blastopore lengthens (Fig. 99 *A*), and is constricted in the middle of its length, where its edges become approximated and fused; thus the original single blastopore becomes divided into two apertures (Fig. 99 *A–C*). During this process, the vacuolated entodermal syncytium becomes arranged into a regular epithelium which, where the blastopore is still patent, passes over into the ectoderm, but in the region of the closed blastopore forms a tube that is said at first to be connected with the mesoderm-bands lying in that region, but to become isolated later, thenceforth forming a distinct entodermal tube.

In *P. novae-zealandiae*, in consequence of the large amount of yolk present, this process is somewhat different. The entoderm-cells are here said to become arranged at the periphery of the yolk into an epithelium which thus surrounds the yolk. The latter would then be gradually absorbed during the further development of the intestine. The mouth and anus form as in *P. capensis* (Sheldon).

The two apertures derived from the elongation and constriction of the blastopore (Fig. 99 *D*) are the primitive mouth and anus. They do not, however, persist as those organs in the adult, owing to the appearance of a depression of the ectoderm at each of the openings, so that the point of union between the ectoderm and the entoderm is shifted inward, and an ectodermal stomodaeum and proctodaeum are formed.

The changes of form undergone by the embryo have their influence on the rudiment of the intestine. As a consequence of the curvature of the embryo, the entoderm extends anteriorly and posteriorly above the mouth and the anus (Fig. 98 *A*). The anterior wall of the stomodaeum thus runs forward. During the further development of the embryo, however, the course changes. When the mouth is shifted more to the anterior end, the anterior entodermal sac degenerates, and the stomodaeum now appears directed posteriorly (Fig. 98 *B*). The dorsal wall of the anterior portion of the intestine up to this point was closely apposed to the body-wall (Fig. 98 *A* and *B*), but the latter now separates from the gut and forms the swollen anterior end of the embryo (Fig. 98 *C*). It is followed in this course by a diverticulum of the entoderm, while the stomodaeum retains its former position. This diverticulum is also obliterated in the further course of development, and the intestine then runs straight back. The stomodaeum gives rise in *Peripatus* to the muscular oesophageal swelling (pharynx), mesodermal tissue also contributing to its formation. The external changes in the mouth have already been described in connection with the external form of the body (Fig. 94, p. 185). The growth of the embryo produces similar changes at the posterior end of the intestine.

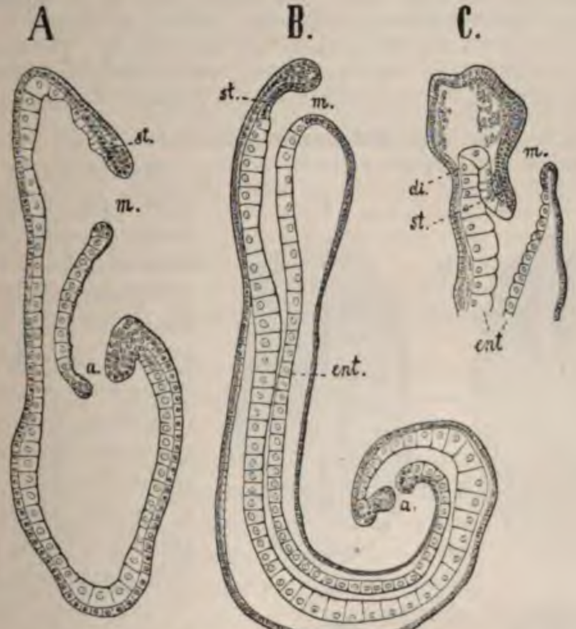

Fig. 98.—Median longitudinal sections through embryos of *P. capensis* at various ages (after Sedgwick). *an*, anus; *di*, anterior entodermal diverticulum; *ent*, entoderm; *m*, mouth; *st*, stomodaeum.

In the American species of *Peripatus*, the intestine even at its first appearance differs from that of *P. capensis*, as no elongation of the blastopore occurs in these forms (v. Kennel). The rudiment of the enteron, which is completely closed to the exterior and has been produced by the ingrowth of cells (Figs. 80, p. 171, and 81, p. 173), is here sac-shaped. As the embryo lengthens, the enteron also extends in the form of a tube. Its connection with the ectoderm is brought about through the fusion of the entoderm with the ectoderm, an invagination of the latter at this point forming the oral aperture. The mouth arises ventrally on the boundary between the head and the trunk, and the anus in front of the blastopore (Fig. 89 *A*). It has already been pointed out (p. 178) that these two apertures occupy the same positions as in *P. capensis*, and that they perhaps were originally related to the blastopore. v. KENNEL, however, does not believe this, and, further, seems little inclined to attribute much value to the observations on this point made in other species of *Peripatus*. He attributes an altogether different significance to the groove in the blastoderm observed by himself and described by us in accordance with the views of English authors as the blastopore.

The further development of the pharynx takes a course similar to that above described, the primary oral aperture shifting inwards, while an anterior entodermal diverticulum appears. The anal aperture, on the contrary, which arose in front of the blastopore through the formation of a slit (Fig. 89 *A*), is said not to coincide with the adult anus. The former closes by the approximation of its edges, and an ectodermal invagination arises a little distance in front of it, grows inward towards the entoderm and fuses with it. The rectum and anus are thus formed, the latter then shifting more to the posterior end of the embryo in consequence of the unequal growth of the latter (v. KENNEL).

The Mesodermal Structures.

The formation of the chief mass of the mesoderm proceeds from a zone of growth lying at the posterior end of the blastopore, and extends forward from this point in the form of two bands (mesoderm-bands) lying symmetrically to the ventral median line. Where a slit-like blastopore is present, as in the African and Australian species, the mesoderm-bands lie in close contact with it, and are thus situated in the region where the ectoderm passes into the entoderm. After the blastopore has partially closed, the posterior (anal) aperture lies in front of the growing zone, and its position is the same in the American species, in which the blastopore is not slit-like.

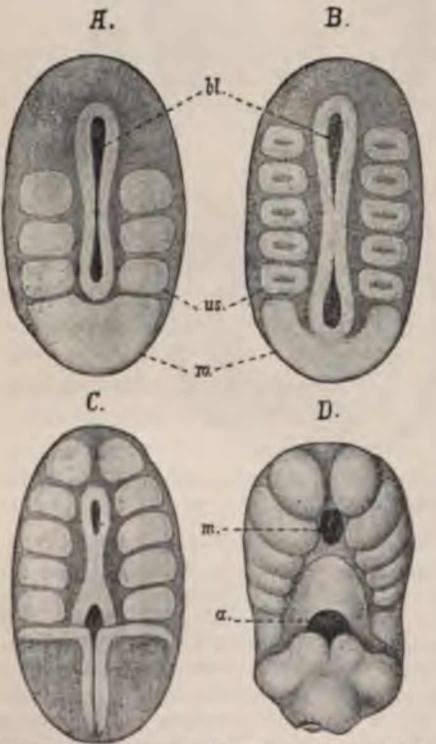

FIG. 99.—Ventral aspect of embryos of *P. capensis*, to illustrate the segmentation of the mesoderm (after BALFOUR and SEDGWICK). *a*, anus; *bl*, blastopore; *m*, mouth; *us*, primitive segments; *w*, zone of growth.

English authors, in accordance with the terminology used in the Vertebrata, have called the growing zone the primitive streak, and the groove-like depression that occurs in it the primitive groove. If such a groove occurs, it must no doubt be regarded as a continuation of the blastopore, and we must assume that it is not the most posterior part which is retained as the anus. The growing point itself must be considered as lying on the posterior margin of the blastopore. At this point, a great accumulation of cells takes place, and the germ-layers are here still fused and undifferentiated. In so far as the mesoderm-bands extend forward from this undifferentiated cell-mass, the condition here to a certain degree resembles that in the Annelida. SEDGWICK even speaks of polar cells of the mesoderm, but of these nothing definite is known. There can be no doubt that the mesoderm is chiefly produced from behind, *i.e.*, from the growing zone, but in consequence of the close apposition of the mesoderm-bands to the edges of the blastopore, the participation of the latter in their growth cannot be excluded (SEDGWICK). In the American species, it appears certain that no such participation occurs. The forward growth of the mesoderm-bands takes place from the point of ingrowth, which must be regarded as the blastopore, and their growth determines the lengthening of the whole embryo. The mesoderm-mass here separates from the sac-like rudiment of the enteron (Figs. 100 and 101), but not so sharply as to exclude a connection of the former with the ectoderm on the one side and with the entoderm on the other, which can be proved to exist even at later stages, when the mesoderm has become far more highly differentiated. The mesoderm may thus be regarded even in this case as arising on the boundary between the ectoderm and the entoderm.

The further development of the mesoderm-bands takes place in a manner very similar to that in which they develop in the Annelida. Before they have reached the anterior end of the blastopore, they break up into paired, regularly arranged segments (Fig. 99 *A–C*, *us*). Cavities then appear in these, and, as these gradually widen, the cell-material of the separate segments becomes arranged into a regular epithelium. The paired primitive segments thus arise. As they extend further, the outer wall becomes applied to the ectoderm and the inner to the entoderm (Fig. 100), like the somatic and splanchnic layers of the Annelida. A pair of primitive segments belongs to each body-segment. The differentiation of the primitive segments commences in the most anterior part of the mesoderm-bands and extends backward, their number increasing with the growth of the body; the first pair of primitive segments to develop is thus that belonging to the cephalic segment, and this is also much larger than any other pair. It extends almost to the ventral and dorsal middle lines; the two halves, however, do not come into contact, and consequently no mesentery is formed. Transverse sections through the body of an embryo at the stage when the primitive segments are being differentiated closely resemble, especially in the anterior and posterior regions, similar sections through an Annelidan embryo;

they show the ectoderm with its ventral thickenings, and the two mesoderm-segments containing the primitive body-cavity, bounded by the epithelial walls, applied to the ectoderm and the entoderm (Fig. 100).

Such anatomical and histological differentiation is present in the embryo represented in Fig. 88, and no further essential change appears until twelve to fifteen segments are visible externally, together with the full (adult) number of internal segments (v. KENNEL).

When the mesoderm-bands have broken up into the series of consecutive primitive segments, the resemblance with the Annelida is very striking, but the further course of development differs, inasmuch as it is not the segmental cavities which yield the body-cavity of the adult, for, in *Peripatus*, the latter arises as a pseudocoele independent of the primitive segments. All that is retained of these segments enters into the formation of the nephridia and the genital organs (v. KENNEL, SEDGWICK).

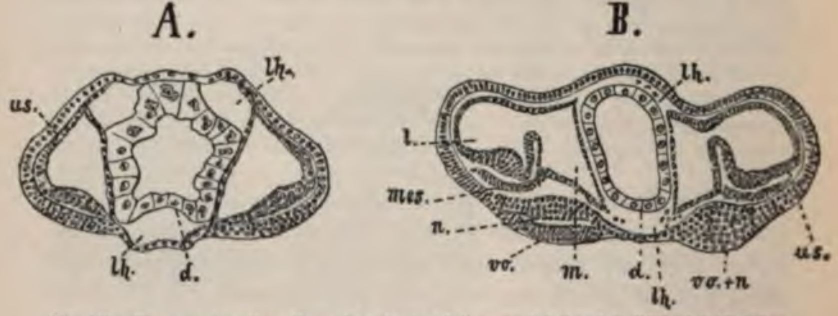

FIG. 100.—Transverse sections through embryos of *P. capensis* (*A*) and *P. Edwardsii* (*B*) (after SEDGWICK and v. KENNEL). *A*, transverse section through the region of the oral papillae in an embryo at about the stage depicted in Fig. 91 *A*. *B*, transverse section through a trunk-segment of a young embryo. *d*, intestine (entoderm); *lh*, dorsal and ventral spaces between ectoderm and entoderm (parts of the primary and adult body-cavity); *l*, lateral, *m*, median portions of the segmental cavities; *mes*, portions of mesoderm detached from the primitive segments; *n*, rudiment of the ventral cord; *us*, primitive segment; *vo*, ventral organ; *vo*+*n*, common thickening of the ventral organ and the ventral nerve-cord.

The formation of the future body-cavity and of the nephridia is commenced by a thickening of the ventral wall of the primitive segments; and subsequently, by an ingrowth of the cells of this thickening, a separation of the segmental cavity into two spaces is brought about, one dorso-median and the other lateral (Fig. 100 *B*, *m* and *l*); these are at first connected, but become completely separated later (Fig. 104 *A*, p. 210). The dorsal portion shifts towards the dorsal median line, while the greater part of the lateral portion is withdrawn into the rudiments of the limbs (Fig. 104, v. KENNEL, SEDGWICK).

Even before this separation has commenced, while the primitive segments still retain their sac-like shape, the antero-dorsal portion of each grows forward over a part of the preceding primitive segment, and thus extends into the preceding body-segment. This explains the fact that in transverse sections we not only see the segmental cavity of the segment through which the section passes, but also a portion of that belonging to the next segment, and that this latter lies above the ventral portion of the segmental cavity of the preceding segment.

The lateral portions of the primitive segments yield the nephridia, and the dorso-median the genital glands in the segments which contain these organs; in the other segments these portions disappear, their cell-elements being used in the formation of the blood vascular system and the musculature, and for the further development of the pseudocoele, which now comes under consideration.

The Body-cavity and the Blood-vascular System.

Even before the division of the primitive segments into two portions, the ectoderm had separated from the entoderm with which it was until then in close contiguity, thus giving rise to a free space dorsally and ventrally to the intestine. These spaces are the first indication of the body-cavity of the adult (Fig. 100 *A* and *B*, *lh*), and into them the mesoderm-cells which become detached from the primitive segments wander. As these cells become applied to the entoderm and ectoderm, the cavity which is at first bounded merely by these two germ-layers, and is therefore to be regarded as the primary body-cavity, becomes lined with mesodermal elements (Fig. 101 *A*, *lh*). These spaces, in consequence of their origin, are not segmented, but the other and lateral portions of the future body-cavity, which arise by separation of the cell-elements in the inner thickened somatic wall of the lateral portions of the primitive segments, exhibit a segmental arrangement (Fig. 101 *A*, *l.lh*). These cavities, at first distinct from one another, fuse together later, and give rise to the two spaces, the lateral sinus of SEDGWICK, which later run continuously through the body, and in which the nerve-strands lie in the adult. Another space on each side of the body agreeing in origin with these latter spaces, develops still more peripherally in the limb-rudiments and surrounds the nephridia (Figs. 101 and 102, *p.lh*). This last part of the body-cavity, which may best be described as the pedal body-cavity, unites later in some places with the lateral spaces, so that, where this is the case, the nephridia and the longitudinal nerves come to lie in one common cavity.

Several cavities unite to form the central space which, in the adult, contains the intestine and the genital organs. According to

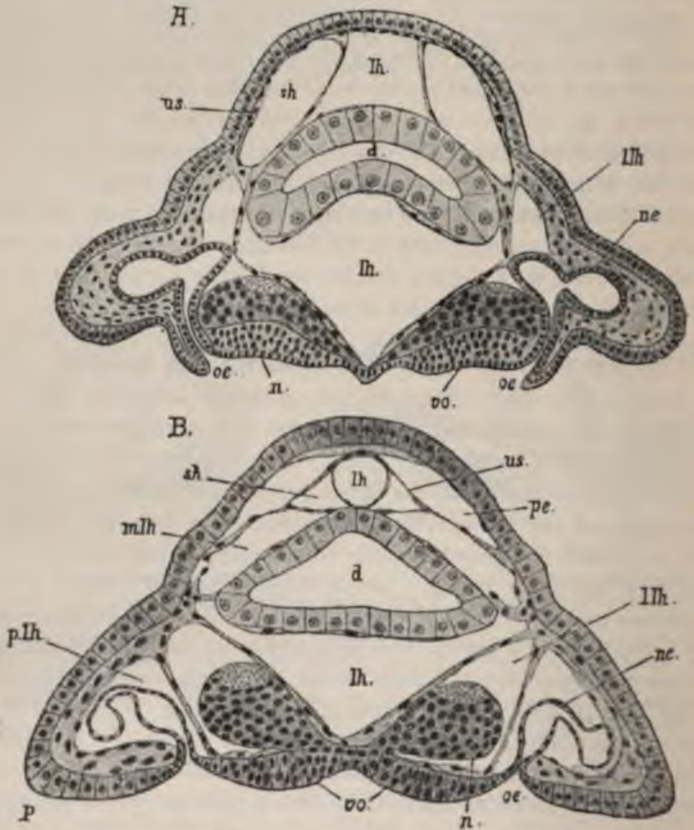

FIG. 101.—Transverse sections through embryos of *P. capensis* at different ages, *A* being taken through the segment of the oral papillae (somewhat diagrammatic, after SEDGWICK). *d*, intestine; *lh*, dorsal and ventral median portions of the body-cavity; *m.lh*, lateral portion of the median body-cavity; *n*, rudiment of the ventral cord; *ne*, nephridia (in *A*, rudiment of the salivary glands); *oe*, external aperture of the same; *p*, limb; *pe*, pericardial cavity; *p.lh*, pedal body-cavity; *sh*, segmental cavity; *us*, dorsal portion of the primitive segments; *vo*, ventral organs.

Sedgwick, two new spaces (Fig. 101 *B*, *pe* and *m.lh*) appear on the outer side of each of the dorsal portions of the primitive segments (*sh*), the wall of which to some extent forms their inner boundary.

The lower of these spaces (*m.lh*) at a later stage grows above the intestine, and unites with its fellow and with the space which has already appeared beneath the intestine (*lh*) to form the greater part of the permanent median cavity, the so-called central compartment of the body-cavity, while the upper one represents (*pe*) the rudiment of the pericardial cavity.

The pericardial spaces on each side extend towards the median line, the remains of the primitive segments being thus displaced downwards. The cavity (*lh*) that arose early above the intestine thus appears confined, together with the dorso-median portions of the primitive segments (*sh*), between the two pericardial spaces (*pe*); the latter grow above the pseudocoele (*lh*), and also between the latter and the dorsal portions (*sh*) of the primitive segments, and unite with one another in the middle line. Thus the common pericardial cavity is formed, surrounding the dorsal pseudocoele (*lh*); the latter now assumes a tubular form and becomes the definitive heart (Fig. 102, *h*). According to SEDGWICK, the primitive segments take no part in the formation of the heart. The ostia of the heart, the formation of which has not been closely observed, do not arise until later, when the embryo is ready for birth.

Detached mesoderm-cells, which become applied to the outer wall of the heart, give rise to the cell-mass within the pericardial cavity, which has been compared to the fat-body of the Insecta. It involuntarily reminds us of the cell-growth on the dorsal vessel of the Annelida, which is probably homologous with the pericardial gland of the Mollusca; but we are prevented from homologising the two structures because the pericardial gland, as an outgrowth of the peritoneal epithelium, lies within the secondary body-cavity, while the cell-mass in *Peripatus* lies outside the latter. The pericardial space in *Peripatus*, like that of other Arthropods, does not correspond to the pericardium of the Mollusca or the coelom of the Annelida. Only its ventral wall (the pericardial septum, Fig. 101 *B*, and 102, *ps*) is perhaps in part formed by the somatic wall of the primitive segments, as is also the case in the Insecta. In *Peripatus*, as in the Arthropoda, the dorsal vessel is in direct communication, in the adult, with the body-cavity, and this fact is explained by the similarity in the development of this system of organs in the two divisions.

In the two anterior (cephalic and maxillary) segments, the transformation of the primitive somites undergoes certain modifications determined by the special form of these parts.

In the maxillary segment, the inner or dorsal part of the primitive somite is not extensive, and fuses with the corresponding part of the succeeding segment which projects into this segment. The different spaces of the permanent body-cavity are here less distinctly developed. The lateral parts of the primitive segments which occupy the rudiments of the jaws undergo considerable thickening of their outer walls, the formation of the strong musculature of the jaws being thus brought about, the inner wall supplies the cells which form the muscles of the pharynx and stomodaeum.

The primitive somites in the cephalic segment are at first very large and occupy the greater part of the segment. As the ventral organs and the brain increase in size, the primitive segments are, however, pressed towards the dorsal surface, and thus become less extensive. Parts of the primitive segments pass into the antennae (as elsewhere into the feet), so that these latter at first appear to be hollow, though the cavity degenerates later (Fig. 96 *A*, *us*). The wall of the first primitive segment gives off cells for the formation of the musculature of the oesophagus. According to Sedgwick, the anterior primitive segment, like the rest, is divided into a dorsal and a lateral portion, the significance of which will be discussed below (*cf.* the Nephridia).

The Musculature.

Even in early stages, before any differentiation had taken place in the primitive segments, cells became detached from them and became applied to the ectoderm. These cells, and others which follow them during the further development of the mesoderm, give rise, immediately below the ectoderm, to a layer of circular muscle-fibres, which at first is thin, but in later stages becomes much thicker (Sedgwick). The longitudinal muscles arise later than the circular fibres, their fibres appearing in the cell-layer that covers the latter internally. According to Sedgwick, they are distributed into various complexes, one ventral, two ventro-lateral, two lateral and two dorsal, corresponding to the longitudinal muscle-bundles of the adult.

The musculature of the intestine and of the inner organs generally is derived from the wandering cells which become detached from the primitive segments and applied to these organs.

The Nephridia.

The nephridia arise in the following way from the lateral portions of the primitive segments, the greater part of which occupy the bases of the limbs. Each primitive segment has a conical outgrowth directed towards the ventral side, which lengthens and, at the base of the foot, fuses with the ectoderm, which becomes perforated at this point, and thus the cavity of the primitive segment opens on to the exterior (Fig. 101 *A*); this aperture persists as the external opening of the nephridium (Sedgwick). The nephridium is now essentially complete (Fig. 101), for it does not possess a funnel opening into the adult body-cavity, as was formerly believed by Balfour and Gaffron, but, according to the latest observations of Sedgwick, throughout life ends blindly in this direction, the canal of the nephridium being continued into the terminal saccular enlargement (Fig. 102, *es*).

We must thus assume that the nephrostome of the Annelida is represented by the opening of the nephridium into the terminal sac. The terminal sac, therefore, corresponds to the coelom (secondary body-cavity of the Annelida), a view which is confirmed by the manner in which the nephridia arise. A part of the coelom has thus come into direct relation to the kidney, and a state of things is found very similar to what has already been met with in the Crustacea (Vol. ii., p. 180), and, with certain modifications, will be found to recur in the Mollusca.

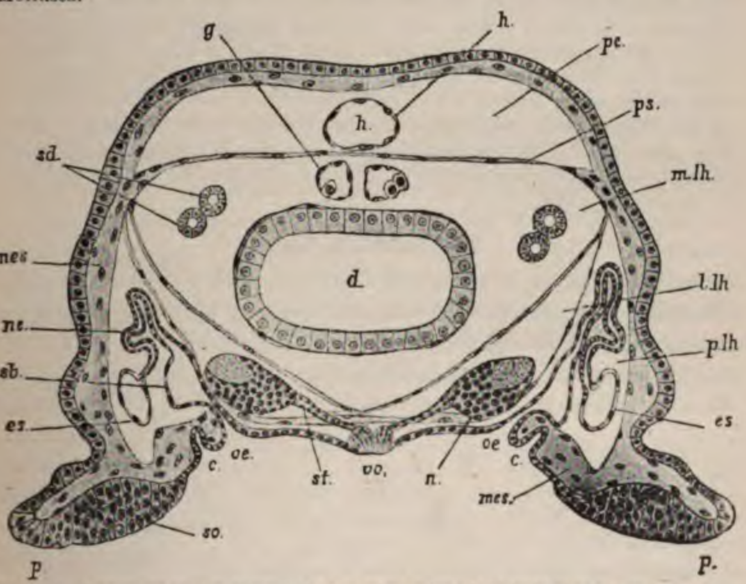

FIG. 102.—Transverse section through the posterior region of the body of an advanced embryo of *P. capensis* (after SEDGWICK, somewhat diagrammatic). *c*, rudiments of the crural glands; *d*, intestine; *es*, end-sacs of the nephridia; *h*, heart; *l.lh*, lateral, *m.lh*, median, *p.lh*, pedal portions of the adult body-cavity; *mes*, mesodermal tissue; *n*, ventral nerve-trunk; *ne*, nephridial canal; *oe*, external aperture of the nephridium; *p*, foot; *pe*, pericardial cavity; *ps*, pericardial septum; *sb*, collecting vesicle (urinary bladder) of the nephridium; *sd*, slime-gland; *so*, sole of the foot (thickening of the ectoderm); *st*, transverse commissure connecting the nerve-trunks (*n*) and the ventral organ (*vo*); *g*, gonad.

The above description of the simple formation of the nephridia applies specially to those of the segments carrying the first to third limbs (of *P. capensis*). Those of the following limbs are distinguished by the fact that the canal becomes much coiled in later stages and widens towards its outer end (SEDGWICK, Fig. 102, *sb*), like the urinary bladder in the nephridia (antennal glands) of the Malacostraca.

Apart from the transformation which we shall find in the nephridia during the formation of the salivary glands and the genital organs, there are important changes to be observed in the cephalic and maxillary segments. In the latter the nephridia have degenerated; traces of them only are said to be found (v. Kennel). In the cephalic segment, on the contrary, the two segmental cavities (in early stages) are said still to open outward through canals (Sheldon, No. 12, Pt. ii.). v. Kennel and Sedgwick describe a (canal-like) continuation of the primitive cephalic cavity which descends on the outer side of the ectodermal thickening (rudiment of the nervous system) and fuses with the ectoderm, immediately in front of the jaws (Sedgwick); according to L. Sheldon, indeed, it even opens outward at this point. This canal has been considered homologous to the canal of the nephridia. According to Sedgwick, it therefore belongs to the lateral portion of the first primitive segment. We cannot clearly make out, from the figures given, the relation of this lateral portion to the coelomic cavity of the antennae. We therefore refrain from discussing the position of this efferent canal as compared with those of the other nephridia, and merely point out that a remarkable change in the position of the nephridium towards the limb must have taken place if this canal is really the nephridial canal of the so-called cephalic segment, and if our former assumption that the antennae of *Peripatus* are transformed limbs is correct (*cf.* p. 186).

The Salivary Glands.

According to v. Kennel and Sedgwick, who agree on this point, there can be no doubt that the paired gland which opens into the buccal cavity through a short, common duct arises from the nephridia of the segment carrying the oral papillae. These ducts develop in the same way as the undoubted nephridia. They originate, after the separation of the dorso-median part, from the lateral portions of the primitive segments which develop an external aperture (Fig. 92, *no*, and 93, *sp*, p. 184). Their further development is peculiar only in so far that the canal, at the point where it passes into the terminal sac, begins to lengthen posteriorly (Fig. 103 *A*), so that a long, blind tube arises at this point (Fig. 103 *B*, *k*). This tube gives origin to the principal part of the salivary gland; it, however, retains throughout life the vesicular portion of the rudiment (*s*) corresponding to the terminal sac (v. Kennel, Sedgwick). The connection of the

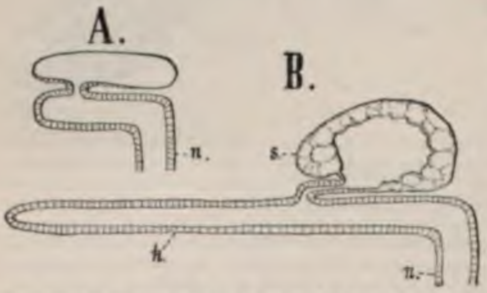

Fig. 103.—Formation of the salivary glands of *P. capensis* (after Sedgwick). *k*, canal of the gland; *n*, nephridial canal; *s*, terminal sac, the walls of which in *A* appear thinner than in *B*.

latter with the glandular tube becomes drawn out into a short canal (Fig. 103 *B*), which enters the latter dorsally (SEDGWICK).

The two external apertures of the nephridia (Fig. 103, *sp*) are displaced into the buccal cavity by the fold which encloses the mouth. They here come to lie in a transverse groove, which, as the buccal cavity develops further, becomes deeper and shorter. This groove eventually becomes a short canal with a slit-like lumen, into which the two nephridial canals (salivary glands) open. This is the common efferent duct of the salivary glands opening into the buccal cavity (v. KENNEL).

The Anal Glands.

The so-called anal glands, a pair of glandular tubes which, in the male of *P. Edwardsii*, open ventrally on either side of the anus, and, in *P. capensis*, open through a short, common efferent duct at the genital aperture,* and are evidently related to the genital apparatus, are shown by their development to be modified nephridia (v. KENNEL). They arise in *P. Edwardsii* from the primitive segments of the last (limbless) segment upon which the anus opens ventrally. The anal glands occur as rudiments in both sexes; in the male only, however, do they attain the functional tubular form; in the female they degenerate.

In *P. capensis*, at the male genital aperture, a pair of glands open which are apparently the homologue of the anal glands of the American species. But since the nephridia of the segment which carries the genital aperture give rise to the efferent ducts of the genital apparatus (see below, p. 209), these glands must have a different origin. It appears probable that they are derived from one of the two additional pairs of primitive segments found by SEDGWICK in *P. capensis* behind the primitive segments of the anal papillae. In this form, the genital aperture has shifted to a position quite near the anus, lying in front of it on the segment carrying the anal papillae. In *P. Edwardsii*, on the contrary, the genital aperture is found two segments further forward, on the penultimate limb-bearing segment. Since, according to SEDGWICK, there are still two segments which remain in an undeveloped condition behind the last fully formed primitive segment (that of the efferent genital ducts), it might be assumed that these corresponded to the last limb-bearing segment and to the so-called anal segment of the American species. The latter would thus have two well-developed segments (the genital segment and that following it) in a region where in the African and New Zealand species a degeneration occurred, which led to the genital and anal apertures coming to lie on apparently one and the same segment. This would also explain the approximation of one of the last pairs of nephridia (the anal glands) to the antepenultimate pair (the efferent genital ducts). This assumption seems to be confirmed by the fact recently made

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* [In *P. novae-britanniae* (WILLEY), the pygidial (anal) glands open by a median aperture situated immediately above the anal orifice.—ED.]

known by L. SHELDON (No. 13) that, in *P. novae-zealandiae*, in the so-called anal segment, there are two coiled glandular tubes, each of which opens independently at the side of the body and laterally to the nerve-trunks, *i.e.*, at a spot where normally the nephridial apertures open. These two glands are the equivalents of the anal glands (SEDGWICK, SHELDON), and are more correctly called accessory glands of the male genital apparatus; from their position, they may safely be regarded as modified nephridia. It should be mentioned further that the American species, which thus shows the more primitive condition in the segmentation of the posterior end of the body, shows on the other hand a less primitive method of reproduction. The shifting of the anus forward from the terminal segment must, indeed, in any case be regarded as secondary.

The Genital Organs.

In the fifteen anterior segments of the embryo of *P. capensis*, the dorso-median portions of the primitive segments are concerned in the formation of the pericardium and heart, but in the following segments their fate is quite different. After their separation from the lateral or nephridial portions, they shift towards the dorsal median line, and, decreasing in size, come to lie as small triangular sacs between the wall of the intestine and the pericardium (Fig. 102, *g*). It is these, according to SEDGWICK, which yield the genital glands. Cells appear in them at a very early stage; these, which are distinguished by their size and specially large nuclei, are the primitive genital cells. We might assume with v. KENNEL, that these arise in the wall of the primitive segments themselves, or in the mesoderm-mass, before it breaks up into primitive segments, as will be described later in connection with the Insecta. On the other hand, SEDGWICK ascribes an entodermal origin to the genital cells. [See Editorial Preface, Vol. II.]

By the fusion of the dorsal portions of the primitive somites pertaining to consecutive body-segments and the breaking through of their transverse walls, two tubes are formed, and these come to lie in the middle division of the body-cavity. Up to this point, the rudiments of the genital organs are alike in the two sexes, but a histological differentiation now takes place, inasmuch as the genital cells increase more rapidly in the male, and become smaller, whereas in the female the germ-cells retain their large size. There is also an anatomical differentiation, the genital rudiments in the female fusing at the anterior end, while in the male they remain distinct in correspondence with the form of the genital apparatus in the adult.

We must assume that the median portions of these posterior primitive segments yield the genital glands, while the efferent ducts are derived from the lateral portions of that primitive segment which develops the genital aperture (in *P. capensis* this is the segment of the anal papillae, and in the American species the antepenultimate segment).* An actual separation into a lateral and a dorso-median section, such as takes place in the other primitive segments, does not, however, occur in the genital segment; here, indeed, the primitive somite extends dorsally, but its widened dorsal portion remains connected with the lateral portion. After this primitive segment, like the rudiments of the nephridia, has acquired an external aperture, its dorsal part fuses with the posterior ends of each of the tubular genital glands, and the rudiment of the genital organs is thus essentially completed. The two external apertures shift towards the middle line so as to lie beside one another. An invagination of the ectoderm then yields the unpaired terminal region (ductus ejaculatorius, vagina) of the genital apparatus.

The development of the genital organs makes it evident that the cavity of the genital glands is homologous with the secondary body-cavity (or coelom). Its cellular lining thus corresponds to the peritoneal epithelium of the Annelida; in both cases the genital products become detached from this, fall into the secondary body-cavity, *i.e.*, in *Peripatus* the cavity of the genital glands, and pass out of the body through the nephridia. That the efferent ducts of the genital apparatus in *Peripatus* are homologous with the nephridia cannot be doubted. This is not only proved by their manner of developing, but is also confirmed by the fact that in the American species the nephridia are wanting in the antepenultimate segment, which carries the genital apertures, while they are regularly developed in the preceding segments and in the segment that follows (GAFFRON).

The transformation of nephridia into efferent genital ducts such as are found in *Peripatus* is of special interest, because of the continuity of the transformed nephridia with the genital glands, and because this demonstrates a similar morphological constitution of the whole of the genital apparatus, such as is met with in other Arthropoda. This continuity tends to mask the nature of the efferent ducts; their true character as nephridia can only be ascertained with certainty from the study of their development.

Another account of the origin of the Mesodermal Structures.

The description given by v. KENNEL of the transformation of the primitive segments differs in some essential points from those of the English authors. Since those points are of great importance, they must be separately discussed.

According to v. KENNEL, besides the cell-growth which, in the form of a fold projecting from below, divides the segmental cavity into two spaces (Fig. 100 *B*, p. 200), a second fold grows in from the inner wall of the cavity (Fig. 104 *A*), so that the cavity is divided into three spaces which for a time are in communication (Fig. 104 *A*, *I*, *II*, *III*). The dorso-median portion (*III*) then becomes partitioned off, and this as well as the greater part of the lateral portion, which lies principally in the foot, is used up in providing elements

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* *Cf.* on this point the remarks on the anal glands, p. 207.

for the formation of the muscles and the connective tissue. The boundaries of the pseudocoele are thus formed, the latter arising on the whole in the way already described by the separation from one another of the primary germ-layers and the formation of cavities in the massive mesodermal tissue, the remaining spaces belonging to the primitive segments naturally being added as their boundary walls break up. The continuity of the lining epithelium is only retained in the middle (ventral) portion (*II*) of the primitive segment. This yields the funnel of the nephridium (Fig. 104 *A–C*, *II*), which, according to this account, as also according to the statements of BALFOUR and GAFFRON, is open towards the adult body-cavity. This funnel, of mesodermal origin, is joined by a ventral invagination of the ectoderm, which proceeds from the base of the foot and grows out like a tube (Fig. 104 *A–C*, *nc*).

FIG. 104.—Portions of sections through embryos of *P. Edwardsii* at various stages (diagrammatic, after v. KENNEL, from LANG'S *Text-book of Comp. Anat.*). *d*, intestine; *l*, foot; *lh*, body-cavity; *m*, mesodermal tissue; *n*, ventral nerve-trunk; *nc*, nephridial canal; *I*, *II*, *III*, the three spaces of the primitive segment-cavity, *II* representing the rudiment of the funnel.

Thus while SEDGWICK derives the whole of the nephridium from the mesoderm, v. KENNEL traces the origin and the greater part of the nephridium to the ectoderm. In our previous description we followed the accounts of BALFOUR and GAFFRON, because, from researches made by BERGH * in connection with the Annelida, it has become highly probable that the nephridia in those animals are formed entirely from the mesoderm.

The derivation of the nephridial canal from the ectoderm must also affect v. KENNEL'S view as to the formation of the genital organs, since he too acknowledged the efferent genital ducts as transformed nephridia. Not only the terminal portion, but the whole of the efferent ducts is therefore of ectodermal origin; only a short piece, connecting the ectodermal uteri and vasa deferentia with the genital glands is yielded by the mesodermal nephridial funnel (Fig. 105 *A–C*, *ml*). From this, in the female, are produced the accessory structures of the uterus. A glance at Fig. 105 *A–C* makes this clear. The female in *P. novae-zealandiae* has a paired receptaculum seminis, and in the American species a paired receptaculum ovorum as well, which opens between the former and the ovary, and close to the latter, into the uterus. These accessory structures are not found in the female in *P. capensis*.

The paired *receptaculum seminis* arises as follows:—Each of the two uteri makes a sharp bend behind the ovary, so that

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* R. S. BERGH, Neue Beiträge zur Embryologie der Anneliden, Theil i., *Zeitschr. f. wiss. Zool.*, Bd. l., 1890; *cf.* also Vol. i., p. 297.

at one point the ascending and descending portions approach each other. As the bent part widens at the same time, fusion and perforation of the wall of the uterus takes place, so that the parts of the uterus in front of and behind the bend enter into direct communication. From this point, however, two canals lead into the widened portion of the uterus, which has thus become vesicular, and forms the receptaculum seminis.

The *receptaculum ovorum* arises between the receptaculum seminis and the ovary as a hernia-like outgrowth of the uterus (or oviduct). When this has attained a certain size, the epithelium at its point is said to rupture (v. Kennel), the so-called ovarial funnel of Gaffron thus arising. This funnel, however, is not, as this author assumes, open towards the body-cavity, but remains covered by the connective tissue which invests the uterus (v. Kennel).

These points seem to require re-investigation. In the meantime, **Sedgwick's** conjecture that the receptaculum ovorum corresponds to the terminal sac of the nephridium of the genital segment seems to merit attention.*

v. **Kennel** agrees with **Sedgwick** as to the formation of the genital glands in so far as he also derives them from the dorso-median portion of the primitive segments, but, if we understand him rightly, he thinks that the dorsal portions of *only two primitive segments*, viz., those belonging to the genital segments, take part in the process; these remain united with the lateral portions (Fig. 105 *A–C*), as **Sedgwick** also showed.

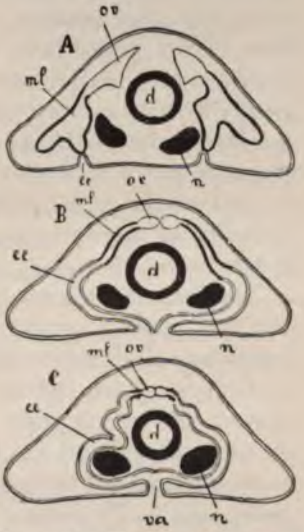

FIG. 105.—Diagrammatic sections through the genital segment of female embryos of *P. Edwardsii* at various ages (after v. Kennel, from Lang's *Text-book of Comp. Anat.*). *d*, intestine; *ee*, nephridial canal (arising through an invagination of the ectoderm); *ml*, mesodermal portion (funnel) of the nephridium; *n*, ventral nerve-trunk; *ov*, ovary (dorso-median portion of the primitive segment); *va*, vagina (unpaired ectodermal invagination).

General Considerations.

The possession of tracheae and segmentally arranged nephridia brings *Peripatus* into relation with the Arthropoda on the one hand and the Annelida on the other. In addition to these two principal characters, *Peripatus* has a number of other

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* [Willey (App. to Lit. on Onychophora, No. II.) supports Sedgwick's views.—Ed.]

features in common with these two divisions, some of these occurring in its ontogeny.

Although the eggs of some species of *Peripatus* have little, or even no yolk, it is highly probable that they are to be traced back to eggs rich in yolk, like those of *P. novae-zealandiae.** These undergo superficial cleavage and become covered with a blastoderm, and thus resemble the eggs of the majority of Arthropods. The long, slit-like blastopore which, in closing, leaves the oral and anal apertures, finds its homologue among the Insecta. The formation of the germ-layers can also be compared with processes found among the Insecta or the Crustacea, but in the development of the mesoderm-bands from the edge of the blastopore and their gradual shifting forwards, and in the nature of the segmentation of these bands, we find an agreement with the Annelida. The same is true with regard to the form of the germ-bands, which is, of course, largely determined by the nature of the mesoderm-bands. BALFOUR pointed out the great similarity between the germ-bands of *Peripatus* and those of the Myriopoda and the Arachnida (*e.g.*, *Geophilus*, *Scorpio*, *Agalena*), which is shown in the form of the limb-rudiments, and especially in that of the cephalic lobes. But we must remember that the formation of such germ-bands was first introduced in the Annelida (*Oligochaeta*, *Hirudinea*).

The great development of the brain and the possession of limbs produces again a greater resemblance to the Arthropoda. This resemblance finds further expression in the union of several segments to form the head, and in the transformation of their appendages (limbs) into mouth-parts. The inclusion of one or more trunk-segments in the head has, indeed, been stated for the Annelida, but these segments are never so radically transformed as in the Arthropoda and in *Peripatus.* Such agreement suggests the question whether the cephalic segments of the Onychophora and those of the Arthropoda may not be homologous, but we are here met with difficulties, the number of the segments involved in the formation of the head differing in the two groups, and the relation of the segments to each other also varying. The latter finds its expression in the composition of the brain. In *Peripatus* the ganglia of the maxillary segment are included in the formation of the brain, which is not the case in the Myriopoda and Insecta. The jaws of *Peripatus* cannot, therefore, be homologised with the

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* [For WILLEY's conclusions (App. to Lit. on Onychophora, No. II.) see footnotes, pp. 165 and 216.—ED.]

mandibles of the Insecta, but this condition in *Peripatus* recalls a similar feature in the Crustacea, in which the ganglia of the second antennae are incorporated in the brain. The second antennae of the Crustacea may thus better be compared with the jaws of *Peripatus.* Then, however, the question arises, whether a segment has not been lost in the Insecta. This point can only be fully discussed later on (ch. xxviii.). Our view of the antenna-bearing segment, and of its relation to that of the Crustacea or of the air-breathing Arthropoda on the one hand, and to the cephalic segment of the Annelida on the other, has already been stated (p. 186), and to this we must refer the reader. We must, however, point out that, in the transformation of the anterior limbs into mouth-parts, *Peripatus* approaches the Arthropoda and is removed from the Annelida, in which the jaws are mere cuticular developments of the stomodaeum.

There can be no doubt that, by the development of limbs armed with claws, *Peripatus* is in advance of the Annelida; on the other hand, the limbs are without the segmentation characteristic of the Arthropoda; the lateral position of the feet also seems a more primitive character inclining towards the Annelida, this character, together with the homonomous segmentation of the body, giving *Peripatus* a worm-like appearance. Another point of resemblance to the Annelida is found in the crural glands, which have no doubt rightly been traced back to the glandular sacs (setiparous glands) of the Annelidan parapodia (BALFOUR). The crural glands are found again in the higher Tracheata, although in these transformed nephridia (coxal glands) have repeatedly been held to be the homologues of the crural glands of *Peripatus.* The passage of the primitive segments into the limbs, which is so characteristic of *Peripatus,* recurs, though not to such a great extent, in the Myriopoda, the lower Insects, and the Arachnida.

When the mesoderm-bands first appear and break up into segments, their wide extension brings about a great resemblance between the embryo of *Peripatus* and the Annelida, though it must not be forgotten that this similarity is greatest just in the species in which the yolk is most reduced, and which we must therefore assume show a derived condition (African and American species).* With regard to the development of the mesoderm, *Peripatus* shows, on the whole, a greater resemblance to the Arthropoda, if the musculature and the segmental repetition of

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* [See footnote, p. 165.—ED.]

the nephridia are left out of account. The muscles, with the exception of those of the jaw, show no transverse striation. They form a dermo-muscular tube composed of several layers of diagonal and longitudinal fibres arranged in symmetrically distributed bands. Here we have features which recall the Annelida far more than the Arthropoda, in which the dermo-muscular tube breaks up into separate groups of muscles distributed in a definite manner. The body-cavity, on the contrary, in its origin (as a pseudocoele), as well as in its final development, is altogether Arthropodan in character. This is also the case with the dorsal vessel, which is connected by ostia with the pericardium, and thus with the pseudocoele, for the pericardial space is, as in the Arthropoda, a part of the pseudocoele, and is formed on the whole in the same manner as that of the Arthropoda. The development of the body-cavity, and its division into separate spaces in the embryo, may be compared with what is found in the ontogeny of the Myriopoda and the Insecta, and may thus be regarded as an important point of agreement between *Peripatus* and these forms (*i.e.*, the Arthropoda generally).

The nephridia seemed to be a specially strong bond of union between *Peripatus* and the Annelida as long as we had to assume that they opened, as in the latter, through a wide funnel into the body-cavity (BALFOUR, GAFFRON). But since it has become known that they are closed by means of a vesicle towards the adult body-cavity (SEDGWICK), although their segmental repetition still offers an important point of comparison with the Annelida, a still greater inclination towards the Arthropoda is shown, the nephridia (antennal and shell-glands) in the Crustacea having the same form.* This similarity of structure renders it probable that the nephridia of *Peripatus* are no longer ciliated†; if, however, the statements that have been made as to the presence of a ciliated epithelium in the nephridia that are transformed in the efferent genital ducts ‡ should

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* [This vesicle or *end-sac* is a thin-walled remnant of the coelom, homologous with that of an Annelid, with which the nephridium communicates by a thick-walled funnel. The body-cavity of the adult *Peripatus* is a pseudocoele like that of other Arthropoda, with which we should certainly not expect to find the nephridia communicating. The nephridia of *Peripatus* are specially interesting since they appear to combine certain Arthropodan features (the coelomic *end-sac*) with others only met with in the Annelida (segmental repetition and marked funnel).—ED.]

† We have not been able to find any definite statements as to the presence or absence of cilia in the nephridia of *Peripatus*.

‡ GAFFRON describes and figures a thickly ciliated epithelium lining the vasa deferentia.

prove correct, this fact would furnish another Annelidan characteristic for *Peripatus*.

The nephridia in *Peripatus*, as in the Annelida, are utilised as efferent ducts of the genital organs. The genital products here, as there, arise in the wall of the secondary body-cavity (which, in *Peripatus*, is very much circumscribed), and pass from it into the funnel of the nephridium. At this point, however, the development of *Peripatus* seems once more to bring it near to the Arthropoda. The ducts unite with the genital glands to form one whole, a condition which, indeed, has already been met with in various divisions of the Annelida.

The structure of the eyes in *Peripatus* and their mode of origin show no connection with the organisation of the Arthropoda, but, on the contrary, agree very closely with that of the Annelida. The eyes closely resemble the eyes of the *Alciopinae*. Further, in comparing *Peripatus* with the Myriopoda, the absence of Malpighian vessels, or, indeed, of any trace of such organs, is a striking peculiarity.

In forming a comprehensive judgment of the anatomical and ontogenetic relationships of *Peripatus*, we have to admit that it unites Annelidan with Arthropodan characters, but that the latter preponderate; not only in its external form, but in its inner organisation, does *Peripatus* appear far more like an Arthropod than an Annelid. Phylogenetically, *Peripatus* may well be considered as an intermediate form in a series beginning with the Annelida and ending with the Insecta, although this does not, of course, imply that *Peripatus* is actually to be regarded as the ancestor of the Myriopoda and the Insecta.

Another peculiarity, worthy of note from an ontogenetic point of view, is the late appearance of the tracheae, the origin of which has not so far been observed even in the oldest embryos, and the interpretation of which is rendered appreciably more difficult by our ignorance of their formation. We can hardly err in tracing them back to ectodermal invaginations, and it therefore seems probable that they are to be derived from modified integumental glands, or, still better, from respiratory portions of the body-covering. Whether we may, from the absence of observations on this point, conclude that the tracheae actually appear very late, or whether we must consider that they have been overlooked, does not appear very certain, but we are inclined to adopt the first of these views, and to explain the late ontogenetic appearance of the tracheae by their late phylogenetic acquisition. The irregular distribution of the tracheae in *Peripatus,* as contrasted with their regular arrangement in the higher Tracheata, seems to indicate a lower condition of the tracheal system, and thus confirms the view that it is newly acquired, and found, in *Peripatus,* to a certain extent in its initial stage.[*]

LITERATURE.

1. Balfour, F. M. The anatomy and development of P. capensis. *Quart. Journ. Micro. Sci.* Vol. xxiii. 1883.
2. Gaffron, E. Beiträge zur Anatomie und Histologie von Peripatus. Theil. i. u. ii. *Schneider's Zool. Beiträge* Bd. i. *Breslau,* 1885.
3. Hutton, F. W. On P. novae-zealandiae. *Ann. Mag. Nat. Hist.* (4). Vol. xviii. 1876.
4. Kennel, J. von. Entwicklungsgeschichte von P. Edwardsii und P. torquatus. Theil. i. u. ii. *Arb. zool. Inst. Univ. Würzburg.* Bd. vii. u. viii. 1885 u. 1886.

[*] [A most important paper dealing with *Peripatus* has recently been published by Willey (App. to Lit. on Onychophora, No. II.). This author, in describing the anatomy and development of a new *Peripatus* (*P. novae-britanniae*), advances such a large series of new facts and fresh interpretations of old ones, that the above account becomes very incomplete without a summary of his results, consequently all students of the Onychophora should refer to this monograph.

Unfortunately, the earliest stages obtained were not well enough preserved to make out the process of cleavage. The egg is small ($\frac{1}{10}$ mm.), without yolk, and enclosed in a remarkably thick egg-membrane. Willey's most important discovery is that at an early stage the embryo has the form of an oval and, for the most part, thin-walled vesicle, only a portion of which gives rise to the embryo, the latter forming a thickened postero-ventral area which becomes, as it were, invaginated into the vesicle. The thin-walled vesicle, which is composed of both ectoderm and entoderm, serves to absorb nourishment and to protect the embryo. Willey regards it as physiologically analogous to the blastodermic vesicle of the Mammalia, and adopts for it Hubrecht's term, trophoblast; it is possibly homologous with the embryonic envelopes of the Insecta. A comparison of Willey's figures with those of v. Kennel and Sclater will show that this trophic vesicle is undoubtedly the homologue of the thin-walled vesicle which encloses the embryo of *P. Edwardsii,* and which v. Kennel derived from the uterine epithelium. Willey's observations thus support those of Sclater on this point. The trophic cavity eventually becomes the gastral cavity, but the embryonic entoderm which was largely used up in the forming of wandering trophocytes (=vitellophags) has to be reconstructed; during this process the entoderm undergoes histolysis, and yolk-granules appear to be formed. Willey regards the yolk of *P. novae-zealandiae* as a secondarily acquired structure, consequently he differs from our author's conclusions regarding the primitive nature of that form, and considers it as one of the more specialised species of *Peripatus*. He does not consider that the large empty trophic vesicle of *P. novae-britanniae* indicates the former existence of yolk, but refers to Hubrecht's conclusions regarding the similar condition in the higher Mammalia which he thinks justify his view, that the presence of yolk in the eggs of *Peripatus* is a very recent secondary condition.—Ed.]

5. Kennel, J. von. Ueber die frühesten Entwicklungsstadien der südamerikanischen Peripatusarten. *Sitzungsber. Naturf. Gesellsch. Dorpat.* Bd. viii. 1888.

6. Moseley, H. N. On the structure and development of P. capensis. *Phil. Trans. Roy. Soc. London.* Vol. clxiv. 1874.

7. Moseley, H. N. Remarks on observations by Capt. Hutton on P. novae-zealandiae, etc. *Ann. Mag. Nat. Hist.* (4). Vol. xix. 1877.

8. Saint Remy, G. Contribution à l'étude du cerveau chez les Arthropodes Trachéates. *Archiv. Zool. Exp.* (ii.). Tom. v. Suppl. 1887–90.

9. Sclater, W. L. On the early stages of the development of a South American Species of Peripatus. *Quart. Journ. Micro. Sci.* Vol. xxviii. 1888.

10. Sedgwick, A. The development of the Cape Species of Peripatus. Parts i.–iv. *Quart. Journ. Micro. Sci.* Vols. xxv.–xxviii. 1885–88.

11. Sedgwick, A. A Monograph of the Species and Distribution of the Genus Peripatus. *Quart. Journ. Micro. Sci.* Vol. xxviii. 1888.

12. Sheldon, L. On the development of P. novae-zealandiae. Parts i. and ii. *Quart. Journ. Micro. Sci.* Vols. xxviii. and xxix. 1888–89

13. Sheldon, L. Notes on the anatomy of P. capensis and P. novae-zealandiae. *Quart. Journ. Micro. Sci.* Vol. xxviii. 1888.

14. Sheldon, L. The maturation of the ovum in the Cape and New Zealand Species of Peripatus. *Quart. Journ. Micro. Sci.* Vol. xxx. 1890.

APPENDIX TO LITERATURE ON ONYCHOPHORA.

I. Dendy, A. Description of Peripatus oviparus. *Proc. Linn. Soc. N.S.W.* Vol. x. 1895.

II. Willey, A. The Anatomy and Development of Peripatus novae-britanniae. *Willey Zoological Results. Cambridge,* 1898.

For recent views on the systematic position of *Peripatus*, see *Nat. Sci.*, Vol. x., pp. 97 and 264, 1897.

CHAPTER XXVI.

MYRIOPODA.

Systematic :—

I. CHILOPODA, with a dorso-ventrally compressed body, two pairs of maxillae, and one pair of maxillipedes; with one pair of limbs on each body-segment; genital aperture on the penultimate segment.

Geophilus, Lithobius, Scolopendra, Scutigera.

II. SYMPHYLA, small delicate forms with only twelve segments, to each of which is added an intermediate segment; with twelve pairs of limbs on the principal segments; with one pair of maxillae, without maxillipedes; genital aperture on the fourth segment; a single pair of branching tracheae opening on the head; at the posterior end, two stylet-like processes (cerci).

Scolopendrella.

III. PAUROPODA, small delicate forms with twelve body-segments, nine of which only carry limbs; with one pair of maxillae; without maxillipedes; characterised by the possession of three long flagellae on the antennae; paired genital apertures situated at the base of the second pair of legs; tracheae not known.

Pauropus.

IV. DIPLOPODA (CHILOGNATHA),* with cylindrical body; with one pair of maxillae (gnathochilarium), without maxillipedes; the fifth and subsequent segments are double, each carrying two pairs of limbs; genital aperture between the second and third pairs of limbs.

Polyxenus, Glomeris, Polydesmus, Strongylosoma, Julus.

Oviposition and the Constitution of the Egg.

The eggs of the Diplopoda are usually laid in large numbers, enclosed in an earthen nest formed by the female, by whom they are watched for a long time, often until the young are hatched.

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* [POCOCK subdivides the Diplopoda into the Pselaphognatha, containing the single family *Polyxenidae*, and the Chilognatha. For recent views on relationship of the Chilopoda and the Diplopoda, see footnote at the end of this chapter. —ED.]

The nests are found in the damp earth, under stones, the bark of trees, etc. The eggs within them may be glued together into large clumps (*Julus*). The *Polyxenidae* surround the heaps of eggs with a thick envelope formed from their own hair. *Glomeris* lays its eggs singly and at wide intervals; each egg is surrounded by the female with a special capsule formed out of earth moistened by a glandular secretion.*

It has been stated that viviparous forms occur among the *Scolopendridae*; but, on the other hand, some of these animals have also been observed to lay eggs in large clusters. In these latter cases it was found that the eggs are taken care of by the female, which rolls itself spirally round them and remains immovable until the young are hatched. *Lithobius* lays its sticky eggs one at a time and rolls them in the soil until they become coated with earth.

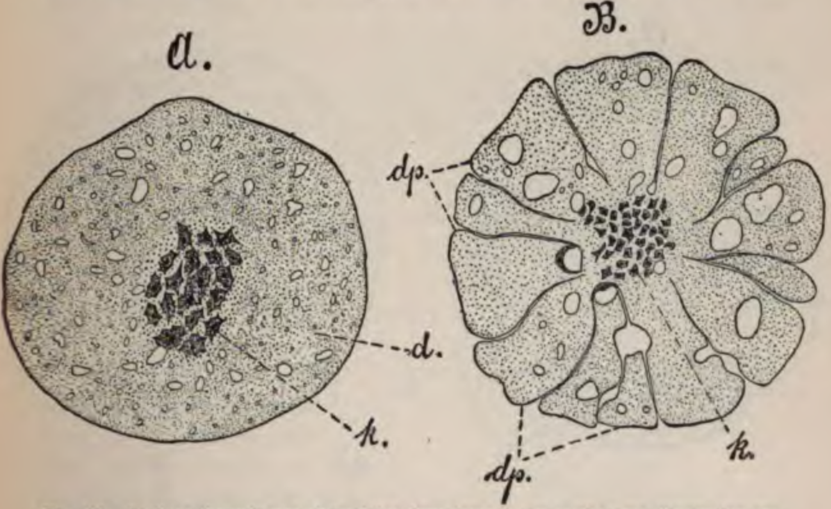

FIG. 106.—Sections through eggs of *Geophilus ferrugineus* at two early stages, illustrating the formation of the blastoderm (after SOGRAFF). *d*, yolk; *dp*, yolk-pyramids; *k*, nuclei, each surrounded with a protoplasmic area.

The eggs, which are usually spherical, seldom oval, are very rich in yolk. They are surrounded by a vitelline membrane and another structureless but firmer envelope, the chorion, which is apparently secreted by the genital ducts.

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* Statements of a more detailed nature as to the time and mode of laying the eggs in the Diplopoda are to be found in the older works of NEWPORT and FABRE, and more especially in two treatises by O. v. RATH (Nos. 16 and 17). Further accounts of the laying of the eggs and the care of the brood are given by LATZEL (No. 10) in his description of different species of Myriopoda.

1. Cleavage and Formation of the Germ-layers.

The cleavage of the Myriopodan egg has repeatedly been described as total, but deserves this designation even less than, for example, the eggs of the Araneae. The egg, it is true, shows a number of segments, which at first is not large, but increases later, and these produce the appearance of division into more or less sharply marked blastomeres, but this appearance is not the expression of total cleavage in the strict meaning of the term, and only arises some time after the division of the cleavage-nucleus and its descendants inside the egg.

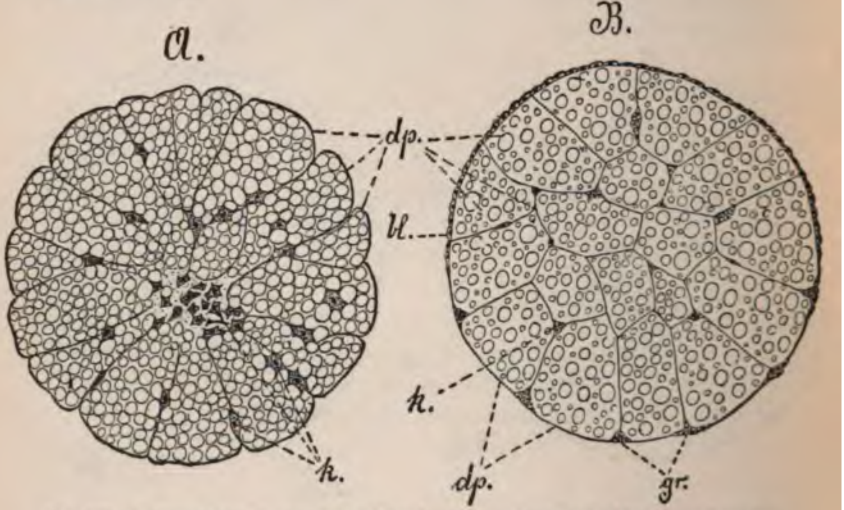

Fig. 107.—Sections through eggs of *Geophilus ferrugineus* showing the blastoderm-formation (after Sograff). *bl*, blastoderm; *dp*, yolk-pyramids; *gr*, groups of blastoderm-cells on the future dorsal surface; *k*, nuclei with the protoplasmic areas surrounding them.

The cleavage of the external surface of the egg does not appear to take place in all Myriopodan eggs. Heathcote, for instance, points out specially, in connection with the *Julus terrestris*, Leach, that no outward segmentation is to be observed in this form, although Metschnikoff, in another species of *Julus* (*J. Morelletti*, Lucas), carefully described and figured the segmentation of the surface of the egg. The absence of this external cleavage in other species is perhaps to be accounted for by the great abundance of yolk in these forms.

The cleavage-nucleus lies, surrounded by a mass of protoplasm, in the centre of the egg. It here divides first into two, and these soon increase by further division, so that many nuclei, each surrounded with an area of protoplasm, are found at this stage in the centre of the egg (Fig. 106 *A*). Only after this has taken place do the separate cell-areas become marked off from one another (Fig. 106 *B*), and thus produce the appearance of total cleavage mentioned above. We may assume that some of the central nuclei had already shifted towards the periphery, and that the cleavage of the egg is a consequence of this. It is probable that the yolk-pyramids which are bounded by the furrows are provided with nuclei, although it has been impossible up to the present time to prove this with certainty. SOGRAFF assumes that the nuclei belonging to the pyramids lie at their tips, and are therefore not far removed from the central nuclei. The yolk-pyramids are not completely marked off from one another, but are connected at the centre of the egg where the central nuclei lie (Fig. 106 *B*).

After the cleavage of the yolk has taken place, a migration of the central nuclei towards the periphery occurs. The nuclei force their way into the yolk-pyramids, the number of which has increased, and shift towards the periphery of the egg (Fig. 107). Judging from SOGRAFF's figures, this migration seems to take place chiefly along the boundaries of the yolk-pyramids (Fig. 107 *A*). Reaching the surface of the egg, the nuclei at first are not evenly distributed, but arranged in groups (METSCHNIKOFF, SOGRAFF, HEATHCOTE), but later they form a continuous layer of cells, the blastoderm. The latter develops first on the ventral surface (Fig. 107 *B*), where the cells divided more quickly, and consequently become smaller, and proceeds from this to the dorsal surface, where, until now, the cells were still arranged in groups (Fig. 107 *B*, *gr*). The yolk-pyramids remain distinct until some time after the formation of the blastoderm.

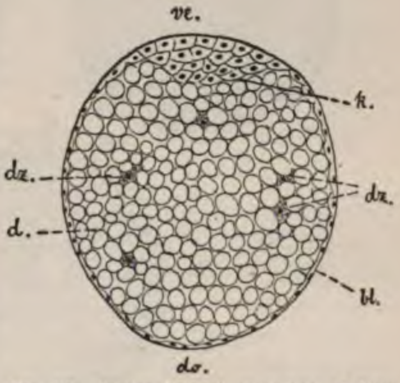

FIG. 108.—Section through an embryo of *Julus terrestris* on the sixteenth day of development, somewhat diagrammatic (after HEATHCOTE). *bl*, blastoderm; *d*, yolk; *do*, dorsal surface; *dz*, yolk-cells; *k*, the keel-shaped accumulation of cells on the ventral side (*ve*).

Most authors agree in assuming that in the formation of the blastoderm a large proportion of the nuclei remain within the egg, perhaps in the yolk-pyramids. This cell-material represents for the most part the entoderm, but is also said to take part in the formation of the mesoderm (SOGRAFF, HEATHCOTE). The latter arises partly as a cell-growth which takes place in the ventro-median portion of the blastoderm. There arises in this region a thickening of the blastoderm projecting inward in the shape of a keel (Fig. 108), in the formation of which cells are said to take part that migrate from the inner part of the egg and become applied to the thickening (HEATHCOTE, SOGRAFF). This thickening is at first median, but divides later into two lateral bands (the mesoderm-bands), which then break up into segments containing cavities.

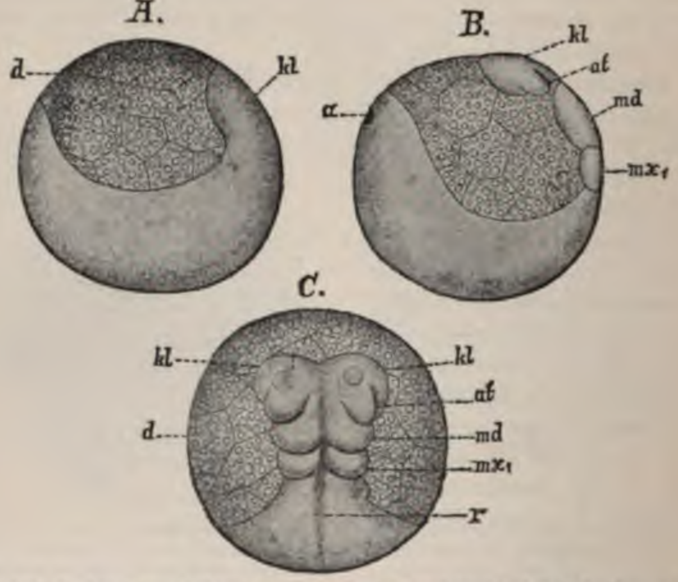

FIG. 109.—Surface views of three early stages in the development of *Geophilus ferrugineus*, showing the rudiment of the germ-band (after SOGRAFF). *A* and *B*, lateral views. *C*, ventral view of the anterior part of the germ-band. *a*, anus; *at*, antenna; *d*, yolk; *kl*, cephalic lobes; *md*, mandibular segment; mx_1, segment of the first pair of maxillae; *r*, median longitudinal groove.

As a longitudinal furrow appeared early in the ventral middle line, the formation of the germ-bands in the Myriopoda might be interpreted in the same way as in *Peripatus*, *i.e.*, the furrow might be regarded as an indication of gastrulation, especially as the mouth and the anus appear at its anterior and posterior ends.

This view, indeed, is in opposition to the statements regarding the origin of the entoderm from cells which have remained in the yolk, but we must remember that similar statements have been made in connection with the Insecta, which later research has not confirmed, and, moreover, the ontogeny of the Myriopoda has not yet been exhaustively investigated, so that nothing definite is known as to the relation of this furrow to the formation of the germ-layers.*

The cleavage and the formation of the germ-layers in the Myriopoda has been investigated by METSCHNIKOFF in various Diplopoda (*Strongylosoma*, *Polydesmus*, *Polyxenus*, and *Julus*, No. 11), as well as in the Chilopoda (*Geophilus*, No. 12); the last-named form has also been investigated by SOGRAFF (Nos. 19 and 20), while HEATHCOTE has re-investigated *Julus* (No. 7). The earliest observations are those of METSCHNIKOFF, but these unfortunately were made without the assistance of sections. SOGRAFF's treatise being in Russian has remained to a certain extent inaccessible to us, and the descriptions of HEATHCOTE are not very satisfactory. Besides these there is a treatise by STECKER on the early development in the Myriopoda (No. 21). The results obtained by this author are, as BALFOUR pointed out, in absolute contradiction to what is otherwise known of the ontogeny of the Myriopoda. This author found no free yolk, and observed a blastula giving rise to an invagination-gastrula with a wide archenteron. It has been conjectured by SOGRAFF (No. 19), that STECKER mistook Gastropod eggs for the eggs of Myriopoda, but this hardly appears possible when we consider STECKER's definite statements as to the species examined by him and his description of their later stages. Further investigations of the genera examined by STECKER have led to totally different results, which justify us in regarding STECKER's account as unreliable and inadmissible in our account of the ontogeny of the Myriopoda.

2. The Development of the External Form of the Body.

A. Chilopoda.

As has already been mentioned, the development of the blastoderm is first completed on the ventral side of the egg, from whence it spreads later to the dorsal side (Fig. 107 *B*). This ventral blastoderm consists of small cells, and here the rudiment of the germ-band appears, its cephalic lobes being first visible (Fig. 109, *kl*). Posteriorly no differentiation can be observed, the rudiment of the germ-band there fading away into the undifferentiated blastoderm, which has not yet completely surrounded the egg. The rudiments of the antennae appear early at the posterior boundary of this first recognisable segment of the germ-band, the cephalic lobes (Fig. 109, *B* and *C*, *at*). The next segment to appear belongs to the mandibles, and then follow the segments of the two pairs of maxillae and the maxillipedes (Fig. 110, *md–mp*). The limbs and segments generally develop in regular order from before backward, as can be clearly made out from Figs. 109 *C*, 110 and 111.

According to SOGRAFF, the anus forms very early in *Geophilus*

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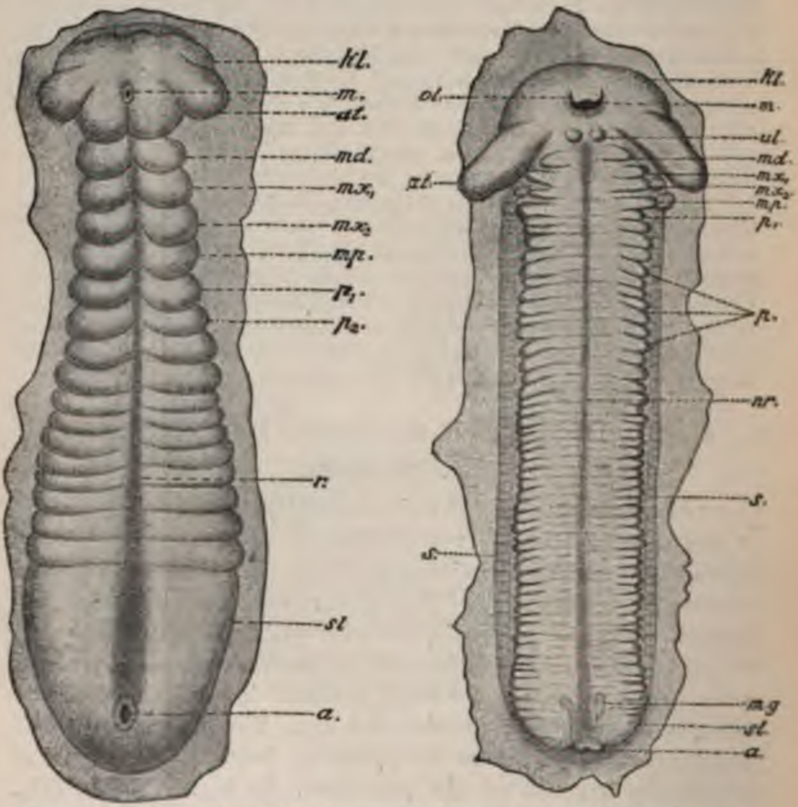
* [HEYMONS (App. to Lit. on Myriopoda, No. III.) states that there is no gastrula-groove in *Scolopendra*; he finds that the entoderm forms both from the yolk-cells and by a budding off of cells from all parts of the blastoderm.—ED.]

(Fig. 109 *B*, *a*). The mouth, on the contrary, is said to appear only at a later stage. It can be seen as an invagination between the cephalic lobes when five segments have developed.

It is difficult to ascertain from the descriptions given whether the oral invagination lies in front of the antennae; this is certainly indicated in Fig. 111 of a *Geophilus* embryo, while in other figures (*e.g.*, Fig. 110) it is not evident. In this latter figure, which represents an earlier stage than Fig. 111, the antennae rather lie in front of the mouth, but another circumstance still to be described in connection with the formation of the organs indicates that the condition here resembles that in *Peripatus*, and that the antennae have



Figs. 110 and 111.—Two stages in the development of the germ-bands of *Geophilus ferrugineus*, unrolled (after Sograff). *a*, anus; *at*, antenna; *kl*, cephalic lobes; *m*, mouth; *md*, mandibles; *m.g*, Malpighian vessels; *mp*, maxillipedes (or segment of the maxillipedes); mx_1, mx_2, first and second maxillae (or segments of the same); *nr*, neural groove; *ol*, upper lip; *p*, legs; p_1, p_2, segments of the first two pairs of legs; *r*, ventral longitudinal groove; *s*, the lateral parts of the germ-bands which already show segmentation; *sl*, caudal lobe; *ul*, paired rudiment of the lower lip.

here, perhaps, as there, the character of post-oral limbs. The difference in the position of the antennae in the two embryos may, perhaps, be explained by imagining a change both of the time and the place of their appearance, such as is occasionally found in other embryonic rudiments.

In the embryo of *Geophilus* depicted in Fig. 111, behind the oral aperture, two somewhat large prominences (*ul*) can be seen, resembling a pair of limbs, but lying in front of the mandibles. SOGRAFF calls these structures the lower lip, but it is not clear whether he actually considers them to be limbs, and to what part of the adult he refers them. The mouth-parts known to us in the Chilopoda only develop behind these, as already seen (Figs. 109–111). Similar structures met with in the Insecta are not regarded as limbs, but as a lower lip.

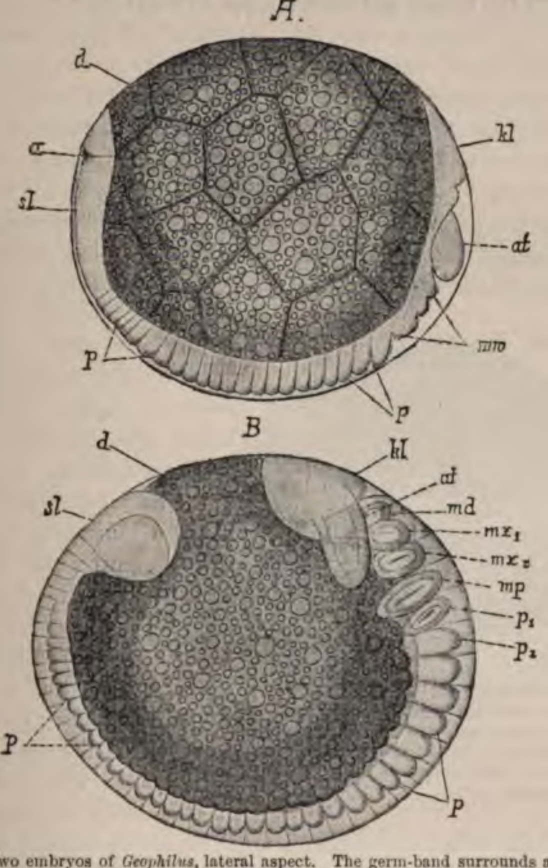


FIG. 112.—Two embryos of *Geophilus*, lateral aspect. The germ-band surrounds a large part of the yolk and still shows the dorsal curvature. The two lateral swellings found in the embryo at the stage depicted in *B* are omitted for the sake of clearness (after METSCHNIKOFF). *a*, anus; *at*, antenna; *d*, yolk; *kl*, cephalic lobe; *md*, mandible; mx_1, mx_2, first and second maxillae; *mp*, maxillipedes; *mw*, mouth-parts; *p* (p_1, p_2), legs; *sl*, caudal lobe.

In the middle of the germ-band a shallow furrow appears (Fig. 109 *C*) extending from the mouth to the anus, the two apertures marking the ends of the furrow (SOGRAFF). This furrow, which soon disappears, naturally invites comparison with the long slit-like blastopore of *Peripatus* on account of its corresponding position and relation to the mouth and anus (*cf.* pp. 175 and 222).

Somewhat later, on each side of the middle line, the rudiments of the ganglionic chain appear as thickenings of the ectoderm also separated by a median furrow (Fig. 111, *nr*). This furrow, however, must not be confounded with the furrow just mentioned, which has disappeared before the formation of the groove now under consideration.

So far the germ-band of *Geophilus*, with its numerous segments, has developed from before backward, and extends with a dorsal curvature round the greater part of the yolk-mass (Fig. 112 *A*). The posterior end at a somewhat later stage grows even further up on to the dorsal side, so as to approach still more nearly the cephalic lobes, as may be seen in Fig. 112 *B*. Now, however, a change takes place, a transverse ventral furrow appearing in the region of the twentieth segment. This furrow deepens considerably (Fig. 113), and finally causes the curvature of the embryo to change completely from a dorsal to a ventral flexure (Fig. 114), This causes the posterior end of the body to separate from the cephalic lobes, and consequently the dorsal surface, which was formerly much shortened, now undergoes extension (Figs. 112 *B*, 113 and 114). The ventral surface of the posterior half of the body now lies exactly opposite to, and parallel with, the anterior half (Fig. 114), so that the tips of the extremities of the one half touch those of the other, and this flexure of the embryo again leads to the approximation of the caudal and cephalic lobes (Fig. 114, *kl* and *sl*).

FIG. 113.—Embryo of *Geophilus ferrugineus* at the stage when the germ-band begins to flex ventrally; seen obliquely from the ventral side (after SOGRAFF). *at*, antenna; *d*, yolk; *ek*, point at which the band bends; *ex*, limbs; *kst*, germ-band.

Up to this point the actual embryo, as the germ-band, has remained distinct from the yolk-mass upon which it lay, as is evident from a glance at Figs. 109–113. The germ-band now, however, extends laterally and grows round the sides of the yolk-mass, so that the dorsal surface of the embryo begins to develop, and its segmentation commences (Fig. 115). At the same time the two halves of the body that lie parallel to one another lengthen, and approach more and more the final shape, although still showing the ventral curvature (Fig. 115).

A cuticle was secreted at the surface of the embryo at an earlier stage. When the embryo assumed the ventral curve, the cuticle did not follow that curvature, but bridged it over, and thus remained somewhat separate from the body. In later stages, the body, as well as the anterior limbs, is found sheathed in this cuticle. The mature embryo is still enveloped in it, and it is only cast off after the egg-shell (Fig. 115, *eh*) has split as the first larval integument. In the *Geophilus* investigated by METSCHNIKOFF, a tooth is found on the cuticle covering the second maxilla (Figs. 114 and 115, *ez*), this, according to METSCHNIKOFF, is used for splitting the egg-envelope, and is cast off with the cuticle. We thus have here a recurrence of the structure known as the egg-tooth in the Araneae (p. 58). The provisional cuticle in any case corresponds to the envelope formed in other Myriopoda at a still earlier stage which surrounds the embryo in the same way as do the blastodermic cuticle, or the deutovum-membrane of the Acarina (*cf.* pp. 97 and 234).

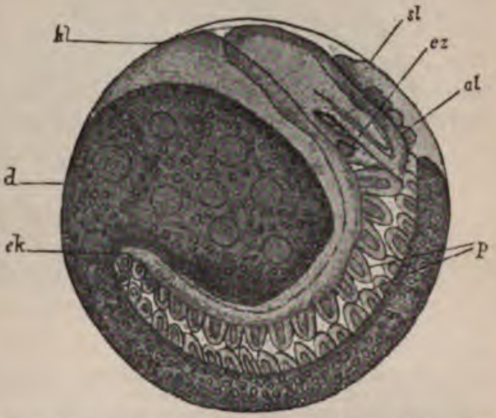


FIG. 114.—Embryo of *Geophilus* after completion of the ventral flexure. The ventral surface of the anterior part of the body is turned towards that of the posterior part, and lies almost parallel to it (after METSCHNIKOFF). *at*, antenna; *d*, yolk; *ek*, point at which the germ-band bends; *ez*, egg-tooth (on the second maxilla); *kl*, cephalic lobe; *p*, legs; *sl*, caudal lobe.

The embryo splits the egg-shell (Fig. 115, *eh*) at an early stage of development. It still retains the ventral curvature and is surrounded by the provisional cuticle. It continues to grow in length at the expense of the yolk now accumulated in the enteron, this growth in length proceeding as before, by the formation of new segments from the still undifferentiated caudal lobe (*cf.* Figs. 112–115). The antennae are now distinctly segmented (Fig. 115, *at*), and the mouth-parts are approaching the adult form, but the other limbs are still simple and truncated. At a stage somewhat later than that depicted in Fig. 115, when the embryo has thrown off the provisional cuticle, METSCHNIKOFF observed the first movements, which consisted of slow extension and flexion of the body. METSCHNIKOFF points out that, in these movements, the extremities might better be compared with the ventral cirri of many Annelids than with the rapidly moving limbs of the Myriopoda.

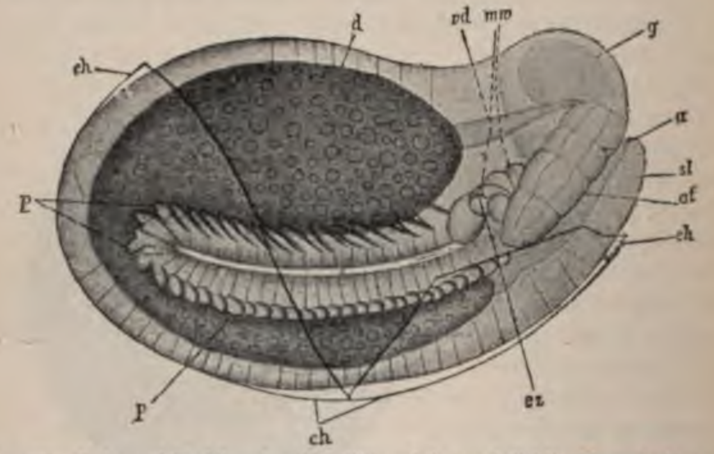


FIG. 115.—Embryo of *Geophilus* after the splitting of the egg-shell (*ch*). The ventral curvature is still retained (after METSCHNIKOFF). *a*, anus; *at*, antenna; *d*, yolk; *ch*, egg-shell; *ez*, egg-tooth on the second maxilla; *g*, brain; *mw*, mouth-parts; *p*, legs; *sl*, caudal lobe; *vd*, stomodaeum.

Throughout the course of development that we have followed, the body of the embryo has been cylindrical, and it retains this shape for a time after it has hatched. It thus resembles in form a Diplopod, until the dorso-ventral flattening of the body characteristic of the Chilopoda takes place. At the stage of hatching, when the "larval integument" is cast, *Geophilus* is said to possess all its limbs, although these are still truncated (Fig. 115) and do not enable it to move with freedom. The young Chilopod probably passes through several moults before attaining the complete form and size of the mother, although when hatched it bears a strong general resemblance to the latter. This is also the case in the *Scolopendridae*, whereas, in the *Scutigeridae* and the *Lithobiidae*, the embryos leave the egg with only seven pairs of legs (not taking into account the maxillipedes). The number of legs is completed during post-embryonic development. But since the young animals in those cases also possess essentially the form of the mother, their post-embryonic development, accomplished through several moults, is fairly simple. The Chilopoda have been divided according to this distinction in the manner of their development into Chilopoda epimorpha (*Scolopendridae*, *Geophilidae*) and Chilopoda anamorpha (*Scutigeridae, Lithobiidae*).

B. Diplopoda.

The embryos of those Diplopoda whose ontogeny has as yet been investigated (*Polyxenus*, *Glomeris*, *Polydesmus*, *Strongylosoma*, *Julus*), leave the egg-envelope at a stage when only comparatively few segments are developed and with only three well-developed pairs of legs (Figs. 121 *B*, p. 235, and 122, p. 237). As contrasted with the Chilopoda, which possess a large number of segments when hatched, the young Diplopoda are thus comparatively far removed from the adult form. They have been distinguished as larvae, but it should be pointed out that, in those parts of the body that are developed, they already show the organisation of the adult.

The First Rudiment of the Embryo.

Flexure of the Germ-band.

Julus. The formation of the germ-band and the first rudiment of the embryo seem to appear in the same way as in *Geophilus*, but the germ-band does not in this case extend so far over the egg, and does not, therefore, assume a marked dorsal flexure. When the cephalic lobes have appeared as rudiments, the stomodaeum lies between them and the proctodaeum, almost at the posterior end of the germ-band, and when, further, the post-cephalic segments have become marked off and show the rudiments of limbs, a transverse furrow appears between the sixth and seventh segments and soon deepens. This is the same process as that which, in *Geophilus*, results in the transition from the dorsal to the ventral curvature (*cf.* Fig. 113). Since, however, the germ-band in *Julus* is small as compared with the mass of the whole egg, the former sinks into the yolk during this process (Fig. 116 *A*). The posterior and still undifferentiated portion of the germ-band now lies bent parallel to the anterior portion, the ventral surfaces of the one half turned towards that of the other (Fig. 116 *A* and *B*).

In the Chilopoda, we were able to trace the inward flexure of the germ-band to the fact that, during the original dorsal curvature of the long germ-band which extends almost entirely round the egg, the development of the dorsal surface is not possible, and consequently the change to the ventral curvature takes place. In consequence of the length of the embryo, the latter is obliged to assume a bent position within the egg. The germ-band of the Diplopoda, however, is short, and the dorsal surface might very well develop without the intervention of the ventral flexure. We nevertheless find the formative processes met with in the Chilopoda recurring in the Diplopoda, and the conditions which, in the former case, were mechanically necessary for the development of the long embryo, are here perhaps rather adapted to the support of the embryo. It is also possible that the larger extent of surface thus brought into contact with the yolk facilitates the nutrition of the embryo. The ventral flexure was thus retained, although its primitive significance is lost. These processes are of special interest when compared with the sinking of the germ-band into the yolk in *Peripatus* (footnote, p. 216) and in the Insecta.

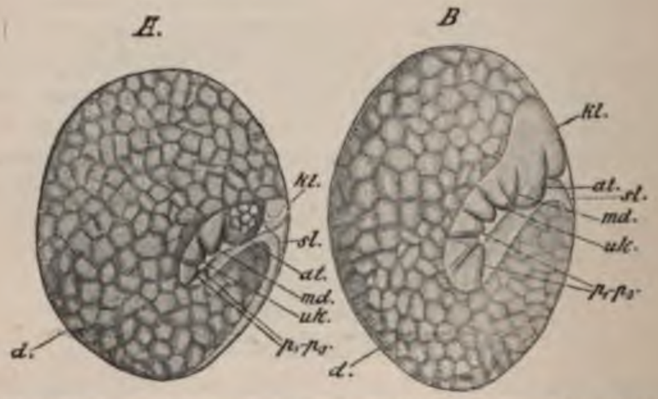


FIG. 116.—Two embryos of *Julus Moreletti*, illustrating the ventral flexure and the sinking of the germ-band into the yolk (after METSCHNIKOFF). *at*, antenna; *d*, yolk; *kl*, cephalic lobe; *md*, mandible; p_1–p_3, first three pairs of legs; *sl*, caudal lobe; *uk*, maxilla.

In *Julus* the invagination of the germ-band takes place only after the rudiments of the antennae, the mouth-parts and three pairs of legs have appeared (Fig. 116 *A*), but in the *Strongylosoma*, *Polydesmus*, and *Polyxenus* it occurs at a very early stage, the change from the condition in the Chilopoda, which is regarded by us as the primitive condition, having advanced still further than in *Julus*.

Of these genera, *Strongylosoma* has been the best investigated, and METSCHNIKOFF has shown that the first indication of the germ-band appears almost in the way that has been described. A transverse furrow, however, seems to appear very early, even before a trace of limb-rudiments is visible. The furrow deepens as in *Geophilus* and *Julus* (Fig. 117 *A*), and here also leads to the ventral curvature of the germ-band (Fig. 117 *B*). In *Strongylosoma* the germ-band does not sink in deep, but in *Polyxenus* it projects somewhat further into the yolk. We can also make out from Fig. 117 *B*, that the whole of the germ-band does not sink into the yolk, as the most anterior and posterior parts of it (cephalic and caudal ends) still remain on the surface. This seems indicated in *Julus* also (Fig. 116).

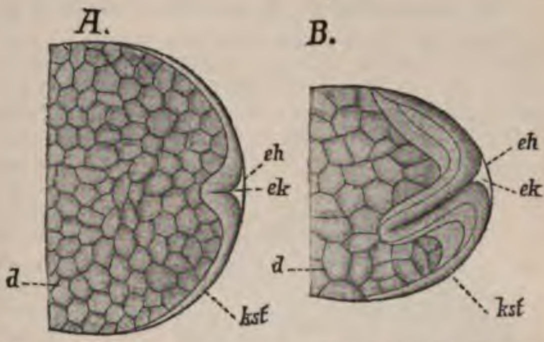


FIG. 117.—Embryos of *Strongylosoma Guerinii* (*A*) and *Polyxenus lagurus* (*B*), to show the early invagination of the germ-band before the appearance of appendages. The dorsal part of the yolk has been omitted. In *B* the lamination of the germ-band due to the formation of the germ-layers can be seen (after METSCHNIKOFF). *d*, yolk; *eh*, egg-shell; *ek*, point at which the germ-band (*kst*) is flexed.

Besides the transverse furrow, METSCHNIKOFF also observed a longitudinal groove extending far forward (and no doubt backward as well) over the germ-band. This groove, which is here somewhat deep, corresponds to that described by SOGRAFF in *Geophilus* as appearing in early stages, but it seems to be much more distinct in *Strongylosoma* than in *Geophilus* (p. 222).

The antennae and mouth-parts very soon develop on the anterior, sunk portion of the germ-band, and the first pair of legs develop posteriorly. In this way a stage is reached similar to that attained by the bending of the germ-band of *Julus* when already provided with limb-rudiments.

The further Development of the Embryo.

Various factors co-operate to bring about the transformation of the ventrally flexed embryo, sunk in the yolk, into the adult form. By the growth of the germ-band towards the dorsal surface, and its simultaneous extension anteriorly and posteriorly, the yolk is taken up into the embryo. The ventral surfaces of the anterior and posterior portions of the body, till now approximated, move apart, and the whole embryo, the dorsal surface of which has also now developed, lengthens somewhat, so that a stage resembling that depicted in Fig. 118 is reached.

The development of the limbs is the next point of importance. It is as difficult here, as in the Chilopoda, to ascertain with certainty the position of the antennae with relation to the mouth. The antennae, as in *Geophilus* (Figs. 114 and 115), are specially highly developed (Fig. 118, *at*). The mandibles also (*md*) are very large. The rudiments of the maxillae are of special importance. According to METSCHNIKOFF's observations, which are confirmed by v. RATH, they arise out of a pair of limb-rudiments following the mandibles (Fig. 116, *uk*), and are themselves immediately followed by the rudiments of the legs (p_1–p_3).

The Interpretation of the Mouth-parts of the Myriopoda.

Whereas the Chilopoda have two pairs of maxillae and one pair of maxillipedes, the Diplopoda possess only one pair of maxillae, which have united to form a lower lip, the gnathochilarium (Fig. 122, *gch*, p. 237), and possess no maxillipedes. The structure of the adult gnathochilarium seems to indicate that it has resulted from the fusion of two pairs of maxillae (Fig. 120, mx_1 and mx_2), and this view has repeatedly been adopted. It is rendered all the more probable by the fact that the Chilopoda have two pairs of maxillae (Fig. 119). These two would be homologous with the first maxillae and the lower lip of the Insecta. Although such an assumption seems both likely and attractive, it has not so far been supported by ontogeny, according to which, as mentioned above, the gnathochilarium is derived from one pair of limbs only (METSCHNIKOFF, No. 11, v. RATH, No. 15). Further investigation of these points is, indeed, very desirable. The structure of the adult mouth-parts, however, seems to lead to a conclusion directly opposed to the above view of the composition of the gnathochilarium out of two pairs of jaws. The gnathochilarium of the Diplopoda (Fig. 120), like the first maxillae of the Chilopoda (Fig. 119, *stm*+*me*+*mi*), is composed of several paired pieces, and there is therefore a certain agreement between them. We may thus perhaps conclude that the whole of the gnathochilarium is homologous with the first

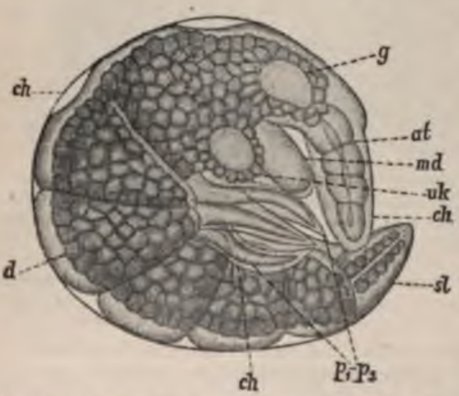


FIG. 118.—Embryo of *Polydesmus complanatus* in a late stage of development. The egg-envelope has been removed (after METSCHNIKOFF). *at*, antenna; *ch*, embryonic cuticle; *d*, yolk; *g*, brain; *md*, mandible; p_1–p_3, first three legs; *sl*, caudal lobe; *uk*, maxilla.

pair of maxillae of the Chilopoda. Another pair of limbs will then have been drawn into the formation of the mouth-parts in these forms, and will have yielded the second maxillae. That such an inclusion of a pair of legs among the mouth-parts is not inadmissible in the Myriopoda is shown by the change of the first pair of legs in the Chilopoda into maxillipedes. The second maxillae of the Chilopoda themselves do not essentially differ from legs (Fig. 119, *pl*), and the fact that, in the Diplopoda, the first pair of legs may shift to a position very near the head (Fig. 122, *b*, p. 237), does not seem without significance.

According to this last view, a comparison of the mouth-parts of the Myriopoda with those of the Insecta would suggest that the gnathochilarium of the Diplopoda and the first maxilla of the Chilopoda should be homologised only with the first maxilla of the Insecta. The second maxilla of the Chilopoda and the first pair of legs of the Diplopoda, on the other hand, would correspond to the lower lip of the Insecta. The external similarity of the plate-like gnathochilarium to the lower lip of many Insects would be explicable not through a direct homology between the two structures, but merely through the similarity of their functions.

The mouth-parts are fully developed even during embryonic life, and therefore have attained their definite form when the young animal hatches (v. Rath, Fig. 122). Three pairs of legs are at first developed in the larva (Fig. 121 *B*), but these do not always appear to belong to three consecutive segments. Thus, in the larvae of *Strongylosoma* and *Polydesmus* (Figs. 121 *B*, and 122), the segment coming next but one after the head carries no limbs; in the larva of *Julus*, this is the case with the third segment (Newport), in keeping with the absence of limbs on that segment in the adult. The third pair of legs is followed by the rudiments of several other limbs, which, however, vary in number in the different forms. These limbs are at first truncated and are hidden under the integument, only appearing as free legs during post-embryonic life. The number of segments has increased posteriorly, so that when hatched, the larva usually has from seven to nine trunk-segments, but the number of these also seems to vary

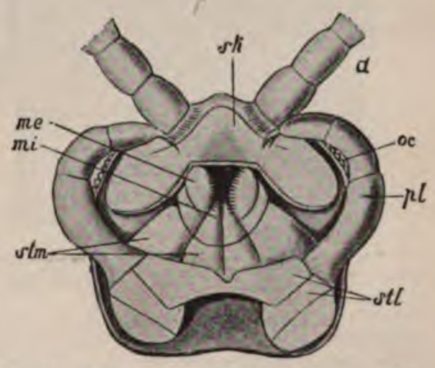


Fig. 119.—The head of *Lithobius validus*, seen from below (after Latzel, from Lang's *Text-book of Comp. Anat.*). *a*, antenna; *me*, outer, *mi*, inner blade of the first pair of maxillae; *pl*, palp of the second pair of maxillae; *oc*, ocelli; *sk*, ventral portion of the cephalic shield; *stl*, basal plates of the second maxillae; *stm*, basal plates of the first maxilla.

slightly in different forms. The segmentation is distinguishable not merely, as in earlier stages, on the ventral surface, but is now continued towards the dorsal side (Fig. 118). When the larva is hatched, its whole body is, as a rule, distinctly segmented (Fig. 121 *B*), though variations occur in this respect.

The **embryonic envelope** of the Diplopoda (and of the Myriopoda generally*) is a structureless cuticle secreted by the superficial ectoderm of the embryo. In *Julus*, its secretion has already taken place before the germ-band shows any signs of segmentation. This membrane which, in its origin, closely resembles the blastodermic cuticle of the Crustacea, forms a sac round the embryo and soon separates somewhat from the surface of the latter. When the germ-band attains its ventral flexure, a corresponding infolding appears in this envelope, which remains somewhat closely apposed to the ventral surface. The cuticle is retained during the course of further development, and still surrounds the embryo like a sac when the latter emerges from the egg-shell. The newly-hatched embryo of *Julus* in consequence somewhat resembles a maggot, as is evident from NEWPORT'S descriptions and figures. This larva, surrounded by the embryonic envelope, is in a lower stage of development than other newly-hatched Diplopods. The head is not distinctly marked off from the body, nor are the segments fully developed, the germ-band not having fully extended over the dorsal surface. At this stage the larva is still incapable of movement, and may be described as a pupa. Beneath the **pupal integument** a

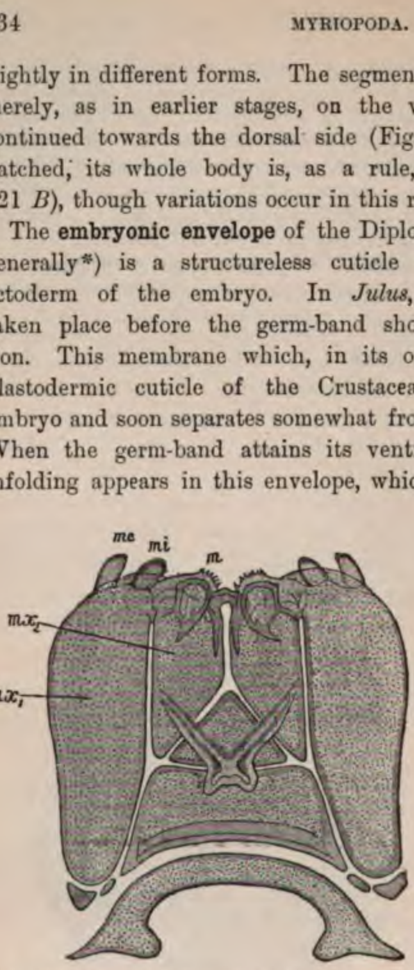


FIG. 120.—The gnathochilarium of *Lysiopetalum carinatum* (after O. v. RATH, from LANG'S *Text-book of Comp. Anat.*). mx_1, base of the outer and inner ridges (*me* and *mi*); mx_2, the so-called tongue-plate which carries anteriorly a toothed blade (*m*); mx_1 and mx_2, have been regarded as corresponding to a first and second pair of maxillae.

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* The embryonic integument of the Chilopoda, according to observation made on *Geophilus*, shows the same characters as that of the Diplopoda (p. 227).

second cuticular envelope is said to rise from the body. This envelope is secreted after the ventral flexure has taken place (HEATHCOTE). Since the limbs were then developed, it no doubt shows outgrowths corresponding to the latter.

The fact that two cuticular envelopes (besides the later cuticular covering of the body) form in *Julus* seems to be evident from METSCHNIKOFF's description, since confirmed by HEATHCOTE, but he does not throw much light on their nature.

The larva of *Julus* passes through a resting stage within the pupal integument, and finally reaches the stage at which other Diplopoda leave the egg. The embryonic or pupal envelope, which has for some time become quite separated from the body, splits, and the larva now for the first time becomes capable of free movement.

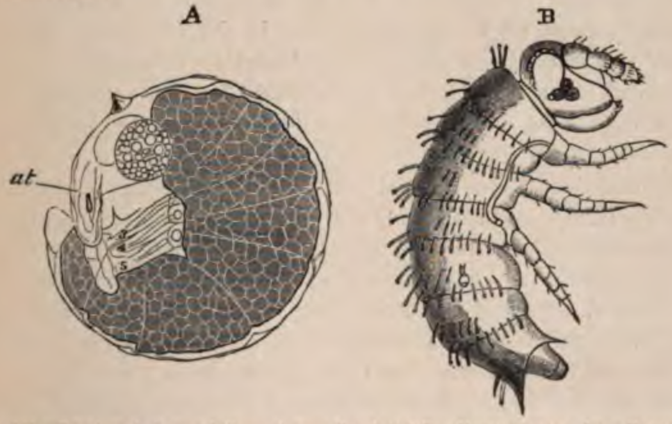

FIG. 121.—Two larval stages of *Strongylosoma Guerinii* (after METSCHNIKOFF, from BALFOUR's *Text-book*). In *A* the larva is surrounded by the cuticular envelope which is provided with the egg-tooth; in *B* it has shed this envelope, and has entered upon free life. *at*, antenna, above and posterior to which, in Fig. *A*, the egg-tooth can be seen; *3*, *4*, *5*, the three pairs of legs of the embryo.

While, in *Julus*, the secretion of the cuticular embryonic envelope takes place specially early, in other forms it occurs later, when the limbs have already appeared as rudiments, so that these become separately ensheathed by it (Fig. 118, *ch*). Its character as a larval envelope is thus more evident. In *Strongylosoma* a special larval organ appears as a cephalic thickening of this envelope in the form of a chitinous cone (Fig. 121 *A*). According to METSCHNIKOFF, this serves for splitting the egg-shell, and may thus be described as an egg-tooth, like the corresponding organ in *Geophilus*. This latter, indeed, belongs to a pair of limbs (Figs. 114 and 115, *ez*), and is thus not homologous with the unpaired egg-tooth of the Diplopoda, which, in form and position, more nearly resembles the unpaired egg-tooth met with in the Opiliones (p. 33), while the egg-tooth of *Geophilus* corresponds in position to the paired structure described in connection with the Araneae (p. 58). Structures functioning in this same way thus occur in the Arthropoda in very different positions.

The egg-tooth is, in any case, cast off later with the larval cuticle. In the embryos of *Polydesmus*, which otherwise closely resemble those of *Strongylosoma*, the egg-tooth is wanting (Fig. 118), no doubt because the egg-integument in this form is much thinner, and a special organ for splitting it is thus rendered unnecessary (METSCHNIKOFF). *Julus* also has no egg-tooth.

The larvae of *Polydesmus* and *Strongylosoma* in a similar way remain (though for a very short time) in the embryonic envelope (Figs. 118 and 121), and are thus also at first incapable of free movement. The pupal stage of *Polyxenus*, on the contrary, could not be discovered, and *Glomeris* also does not seem to pass through such a stage (VOM RATH).

It need hardly be pointed out how strongly the blastodermic cuticle of the Crustacea, and still more the deutovum-membrane of the Acarina, are recalled by the cuticular integument of the Myriopod embryo. The resemblance to the deutovum-membrane is increased by the discovery in *Polyxenus* of free amoeboid cells, like the haemamoebae of the Acarina (Fig. 53, p. 99), outside the embryo and between it and the egg-integument (or the cuticle, where this is present) (METSCHNIKOFF). We must, however, regard this merely as an analogous condition.

Post-embryonic Development.

Stages of post-embryonic development are represented even while the embryo is still enclosed within the cuticular envelope, for the embryo in many cases leaves the egg surrounded by this integument, and must therefore already be regarded as a larva, and the envelope as a larval integument (Fig. 121, p. 235). It has already been mentioned that the so-called larva of the Diplopoda, apart from the small number of its segments, does not differ greatly in form from the adult. The possession of three pairs of legs brings about a striking resemblance to an Insect larva; VOM RATH points out especially its resemblance to the young Podurid. This is of course merely an external resemblance, for, in the first place, the homology of the cephalic regions of the Insecta and the Myriopoda (in respect of the number of segments utilised in the formation of the head) is still very doubtful (p. 232), and further, in the latter, one of the anterior trunk-segments, usually the second, is, as a rule, devoid of extremities (Figs. 121 and 122),* so that the first three pairs of legs are distributed on four segments, whereas the thorax of the Insecta, as is well known, consists of three segments, each possessing a pair of limbs.

The transformation of the larva into the adult, the so-called anamorphosis of the Diplopoda, has been a frequent subject of investigation (NEWPORT, FABRE, BODE, LATZEL, VOM RATH, and others). Variations occur in different forms, but these are not of such importance as to require special attention from us. The most important features of the post-embryonic development are the addition of new segments and the manner in which the double segment characteristic of the Diplopoda originates. The formation of new somites always takes place between the anal segment and that last developed (LATZEL), and the formation of double segments is now proved to be due to the fusion of two of the originally distinct primitive segments (HEATHCOTE).

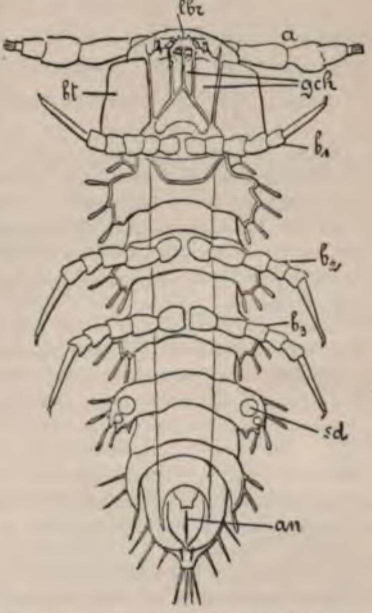

FIG. 122.—Newly-hatched larva of *Polydesmus complanatus* (after O. VOM RATH, from LANG'S *Text-book of Comp. Anat.*). *a*, antenna; *an*, anus; b_1–b_3, the three pairs of legs of the larva; *bt*, cheeks; *gch*, gnathochilarium; *lbr*, labrum; *sd*, the stink-glands.

As already mentioned, the six-limbed larva has several other pairs of legs as rudiments beneath the integument. The number of these varies in different forms. The larva of *Glomeris* when hatched, behind the three anterior well-developed pairs of legs, has five more pairs of truncated, freely projecting limbs (VOM RATH). Thus the *Glomeris* larva, which is said not to pass through a pupal stage, corresponds in this respect to a stage of development attained by other Diplopoda only after several moults.

The first three pairs of legs in the larva of *Polydesmus* (LATZEL, VOM RATH)

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* [In *Polydesmus* the second trunk-segment is devoid of limbs both in the larval and adult condition.—ED.]

are found on the first, third, and fourth trunk-segments (Fig. 122).* Two truncated pairs of legs lying below the integument belong to the fifth segment, and another pair of the same kind to the sixth segment. After ecdysis these limbs project freely, and the stage with seven segments and three pairs of legs is followed by one with nine segments and six pairs of legs. The next (third) stage has twelve segments and ten (♂) or eleven (♀) pairs of legs. The sixth segment now has one instead of two pairs, and the seventh segment of the female has two pairs, while in the male it carries only one. The copulatory limbs of the male which lie on the seventh segment develop only in the adult. The further development of segments and limbs is set forth in the following table:—

Stage I.	7	segments	3	pairs of legs.		
II.	9	„	6	„		
III.	12	„	10	„	(♂),	11 (♀).
IV.	15	„	16	„	„	17 „
V.	17	„	22	„	„	23 „
VI.	18	„	26	„	„	27 „
VII.	19	„	28	„	„	29 „
VIII.	20	„	30	„	„	31 „

Sexual maturity is reached in the eighth stage, and is accompanied by the development of the copulatory limbs which usually belong to the seventh trunk-segment in the Diplopoda. A moult occurs between each stage.

In the *Julidae* examined with special care by NEWPORT in this connection, the course of development was, on the whole, similar to the above. On both the fifth and sixth segments the larva has two truncated pairs of legs beneath the integument, which, after the first moult, appear as well-developed limbs. Through later moults each of the following segments also develops two pairs of legs, and the number of segments increases from before backward.

In both the larval and the adult condition of *Strongylosoma*, *Polydesmus*, and *Julus*, one of the four anterior segments is without limbs, this being the second segment in the first two genera, while in *Julus* it is the third (Figs. 121 *B* and 122). In *Polyxenus* this seems not to be the case; the larva of this Diplopod has at first only five trunk-segments (the anal segment included) and three pairs of legs attached to the three anterior segments. In the next stage the number of segments is the same, but another pair of legs appears on the fourth segment (BODE). This last pair is retained as a single pair when, in the third stage, a pair develops on the newly-formed fifth segment, and during the moult which follows another pair is added on this last segment. During the eight stages passed through by this larva, three other segments, each provided with two pairs of legs (the sixth, seventh, and eighth), are added, the ninth segment, however, carries only one pair of limbs, while the segment lying in front of the anal segment is devoid of extremities (BODE, LATZEL, VOM RATH). It is characteristic of the terminal segment in the Diplopoda that no fusion takes place in it, and this is also the case with the four anterior segments (known as the thorax), and, apparently, fusion is also absent in the genital segment.

C. Symphyla and Pauropoda.

Up to the present time, as far as we know, nothing is known of the embryonic development of these Myriopoda which, on account of their minute size, are

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* [See footnote, p. 237.—ED.]

very difficult to examine. The larvae of *Pauropus*, like those of the Diplopoda, have at first six pairs of limbs (LUBBOCK, RYDER, LATZEL).* The second and third pairs of legs are said to belong to one segment or rather double segment. The larva has only a few segments, there being only one limbless segment besides the anal segment. During the first moult two more pairs of legs appear, and the larva then develops six, seven, eight, and finally nine pairs.

Still less is known of the development of *Scolopendrella*, although such knowledge would be of great value, seeing that special significance attaches to this form. The youngest stage as yet observed had six pairs of legs, but it is not impossible that this stage was preceded by others with fewer pairs (LATZEL). Each of the numerous moults that follow is accompanied by the addition of a new pair of legs, until the full number of segments found in the sexually mature animal is reached. According to LATZEL, the course of development of *Scolopendrella* strongly recalls that of the *Polyxenidae*.

3. The Formation of the Organs.

Our knowledge of the formation of the organs in the Myriopoda is still very incomplete. As far as we know, it appears to take place in a somewhat similar way in the Chilopoda and the Diplopoda. The statements made on this subject by METSCHNIKOFF in his earlier works have been followed by more detailed though not exhaustive accounts by SOGRAFF and HEATHCOTE.†

The Nervous System.

All that we know of the **supra-oesophageal ganglion** is that it has a paired origin in thickenings of the cephalic lobes which finally separate from the ectoderm. At the time when the embryo of the *Julus* leaves the egg-shell, therefore long after the rudiment of the brain has appeared, two pit-like depressions can be seen in the cephalic lobes, resembling those met with in *Peripatus*, the Insecta and the Arachnida (*cf.* Figs. 93, 94 *C*, 28 *B*, and 109 *C*). These depressions are at first shallow, but deepen later, and sink into the rudiment of the supra-oesophageal ganglion, the cells forming the floors of the pits seeming to fuse with the cell-material of this latter. The apertures of the pits narrow, and they become closed vesicles (HEATHCOTE). This formation of ectodermal vesicles in connection with the rudiment of the brain specially recalls the condition of the so-called ventral organ in *Peripatus* (Fig. 96 *B*, p. 190). The vesicles finally disappear, and their significance has not been definitely established, but we may, taking into account the conditions prevailing in the Insecta and Arachnida (p. 62), suppose that

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* For more detailed statements on this subject we refer the reader to LATZEL's work (No. 10, Bd. ii., p. 21), where also the literature relating to it is quoted.

† [See HEYMON's more recent work on the Chilopoda, an abstract of which is appended to p. 257.—ED.]

they are connected with the formation of the optic ganglion. In *Peripatus*, indeed, the pits that appear in the head of the embryo are said to have another significance (p. 190), and this is perhaps the reason why SOGRAFF regards the cephalic pits, which are also present in *Geophilus* (Fig. 169 *C*), as an atavistic feature in no way connected with the formation of the supra-oesophageal ganglion.

The **ventral chain of ganglia** arises, as in other Arthropods, in the form of two strand-like thickenings near the middle line, which show swellings (ganglia) corresponding to the different segments of the body. The median furrow, which lies between the two strands (Fig. 111, p. 224), must not be confounded with the former extremely transitory shallow longitudinal furrow regarded as the blastopore. In consequence of the appearance of the two lateral ectodermal thickenings this second furrow forms in the same position (Fig. 111, *nr*). In *Geophilus* this furrow attains a considerable depth, since the two thickenings on each side of it are large and very near each other. It thus appears as if this central area also took part in the formation of the chain of ganglia, and ought therefore to be called the neural groove. In the Diplopoda, especially in *Julus*, the neural groove is less distinct, but here also possesses the same significance, since the ganglia which become detached from the ectoderm are connected by transverse commissures. The middle strand would thus yield the transverse commissures.

After the ganglia have become detached from the ectoderm in *Julus* (Fig. 126 *A* and *B*), depressions are said to appear in them in such a way that each ganglion is provided with an outwardly directed pit. This process, which is described by HEATHCOTE, is difficult to understand because it takes place only after the detachment from the ectoderm; we should otherwise be reminded of the ventral organs of *Peripatus* (p. 189). The pits which, as in the supra-oesophageal ganglion, become closed vesicles, soon disappear.

In the Diplopoda, the two series of ganglia at first lie somewhat further apart, a fact no doubt connected with the circumcrescence of the yolk by the germ-band; they then draw nearer each other until they come into close contact, and fibrous substance appears on their dorsal side, a feature already described in *Peripatus* (p. 192).

The differentiation of the ganglia takes place from before backward, so that in the posterior, and as yet but slightly developed portion of the body of the growing embryo or larva, the undifferentiated rudiments of the ventral chain of ganglia are found from which new ganglia are abstricted anteriorly (Figs. 124 and 125). In the Diplopoda the larger number of body-segments have two pairs of ganglia, and are thus shown to be double segments.

In the anterior part of the ganglionic chain a fusion which takes place between several pairs of ganglia leads to the formation of the sub-oesophageal ganglion (Fig. 124, *usg*), with which a few more may unite.

As far as we know, no light has as yet been thrown by ontogeny on the subject of the inclusion of the ganglia of true trunk-segments with the brain. The fact that the most posterior section of the brain (the so-called tritocerebrum), forms a part of the circum-oesophageal commissure, and may also possess a special transverse commissure (as in the Diplopoda and *Scutigera*, according to St. Remy), however, perhaps indicates that the tritocerebrum had an origin similar to that of the maxillary ganglia of *Peripatus* and the antennary ganglia of the Crustacea, both of which represent trunk-ganglia secondarily united with the brain (p. 193; Vol. ii., p. 164). A diagram of the Myriopodan brain would closely resemble Fig. 97 (p. 193) of the brain in an embryo of *Peripatus*.*

The Eyes.

The formation of the eyes has been followed in *Julus terrestris*, a form which possesses a large number of ocelli (about forty) on each side of the head. These appear one after the other. The first ocellus appears on the fourth day of free larval life, *i.e.*, after the larva is freed from the cuticular envelope, and is followed gradually by the others until the full number is reached. According to Heathcote, the first step in the formation of the eye is an ectodermal thickening which arises behind the base of the antenna, and in which pigment is deposited. A cavity then forms in the thickened part, so that the whole appears as an optic vesicle. As the cavity increases

FIG. 123.—Section through a developing eye of *Julus terrestris* (after Heathcote). *ch*, chitinous covering of the body; *h*, ectoderm beneath the lens (lentigen layer); *hyp*, ectoderm (hypodermis); *k*, mesodermal capsule; *l*, lens; *r*, retina.

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* [In *Scolopendra*, according to Heymons (No. III.), the protocerebrum consists of (1) the archicerebrum arising in the clypeus, (2) two pairs of ganglia in the primary head-plate, (3) the optic ganglia, (4) a pair of ganglia in the antennular segment. The deutocerebrum is derived from the antennary ganglia, while the tritocerebrum arises in the limbless segment intercalated between the antennal and mandibular segments. This shows that at least one pair of trunk-ganglia (two if the antennae are really trunk-appendages) is incorporated in the adult brain.—Ed.]

the outer wall becomes thinner while the inner wall thickens. The whole of the latter yields the retina, and the former secretes the lens. According to this author this outer layer has not the significance of a vitreous body-layer, but only functions to secrete the lens, and at a later stage degenerates (Fig. 123, *h*). Between the regularly arranged cells of the future retina, Heathcote found smaller cells of irregular form resembling amoeboid mesoderm-cells, and he assumes that these wander in among the ectodermal retinal elements and function as pigment-cells. A layer of mesodermal-cells becomes closely applied to the retina, forming a capsule round the optic cup (Fig. 123, *k*).

Heathcote's account of the rise of the Myriopodan eye does not sufficiently explain either its manner of development, or the relation of the ontogenetic stages to the adult eye. It is specially important to ascertain the significance of the outer layer of cells lying beneath the lens (Fig. 123, *h*) in the adult eye, or at least to prove its presence. A species of *Julus* examined by Grenacher has a unilaminar basin-shaped eye, devoid of the vitreous layer. Other Myriopoda, especially Chilopoda as it appears, have the vitreous body, and thus have bilaminar eyes. These eyes thus differ somewhat from ocelli of the simplest kind such as occur in other Myriopoda. It would therefore be important to prove whether the rudiment of the eye is actually a closed vesicle, or whether it is not rather an ectodermal depression, such as it appears to be still in the adult in the case of eyes devoid of the vitreous body. The vitreous body in such cases would have to be explained as arising, as in the ocelli of the insect larvae (Fig. 36), by the ingrowth of ectoderm from the sides.

As we have already seen (p. 194), the eyes of *Peripatus* arise as ectodermal depressions, and it seems the simplest explanation if we can trace back the basin-shaped eyes of the Myriopoda as well as the ocelli of the Insecta to a similar primitive method of development resembling that of the Annelidan eyes (p. 69). The Myriopoda, indeed, are of special interest in this connection, inasmuch as some of them possess only a few ocelli (*Scolopendra*, for example, has only four on each side), while a larger number is found in others, leading to the formation of so-called crowded ocelli (thirty to forty and more, in *Lithobius*, *Julus*, Fig. 119, *oc*), till finally a compound eye results, consisting of numerous single eyes (about 200 in *Scutigera*), and resembling a facet-eye like that of *Limulus*. This may even show a kind of rhabdom-formation without belying its relation to the crowded ocelli of other Myriopoda. We thus appear to have, in the Myriopodan eyes, the different stages indicated by us as of probable occurrence in the phylogeny of the facetted (polymeniscus) eye when we were considering the Arachnidan eye (p. 69).[*] Careful ontogenetic and morphological investigation of these points is exceedingly desirable, and would no doubt have a successful issue.

[*] [Recent investigations on the structure of the eyes of *Scolopendra* and *Scutigera* (Nos. I., VII., XI.) entirely confirm this suggestion. The eye of *Scolopendra* consists of a few perfectly distinct ocelli, each of which exhibits the structure typical of that class of eye, being a simple ectodermal depression with lateral vitreous body and numerous retinulae, each with a rhabdom projecting into the cavity of the eye, the whole being overlaid by a cuticular lens. In *Scutigera*, on the other hand, the ocelli are greatly modified by mutual pressure until they have almost assumed the character of the ommatidia of a

The Tracheae.

The tracheae develop late. In *Geophilus*, the embryo has no tracheae when it leaves the egg, and respiration at first takes place through the covering of the body, which is still very thin (SOGRAFF). In the Diplopoda also, the tracheae appear late, apparently only after the embryo has split the chorion, and is lying in its pupal integument. In *Julus*, there is at this stage, behind the base of each leg, a pit-like depression which deepens and forms two diverticula, one of which extends into the space beneath the ventral chain of ganglia, while the other grows out dorsally. These are the two principal trunks proceeding from the tracheal sac, and give rise to the tracheal tubes which are lined with a chitinous intima.

In the Diplopoda, each trunk-segment has two pairs of stigmata, each leading into a tracheal sac, from which originate bundles of simple tracheal tubes. The tracheal tubes do not branch, nor do they anastomose; they thus exhibit a very primitive form. The presence of two pairs of stigmata on each segment in the Diplopoda is an additional reason for regarding the segments as arising by the fusion of two originally distinct somites.

The tracheae of the Chilopoda are more complicated, as they form branches and anastomose. The distribution of the stigmata over the segments is no longer so regular, though, as a rule, a single pair open on the pleural membrane of most segments, but in some segments they are wanting. *Scutigera* has only a single median dorsal stigma on each segment; in the Symphyla there are only two stigmata, which are situated on the head. In this respect the Chilopoda appear as the less primitive forms.

The Protective Glands.

In the Diplopod larva with three pairs of legs, a pair of depressions appear laterally on the fifth trunk-segment; these are the *foramina repugnatoria* which lead into flask-shaped ectodermal invaginations representing the first pair of stink- or protective glands (Fig. 122, *sd*).

As the segments increase in number, more of these glands develop; each of the double segments contains one pair only, they are never found in the anterior single segments (HEATHCOTE, METSCHNIKOFF).*

compound eye. The retinulae have been greatly reduced in number, and each has become elongated in the plane of the depression of the original ocellus. Two sets of these retinulae can be recognised. A lower set, consisting of three cells only, forms an elongate trifoliate stalk to the ocellus, the rhabdoms of these three cells being correspondingly elongated and in contact with one another. The outer set are more numerous, consisting of twelve cells whose rhabdoms are widely separated by the development of a crystalline cone formed by the fusion of five to seven cells, which are perhaps the representatives of the vitreous body. The whole is covered by a cuticular lens. The eye of *Scutigera* is regarded as intermediate in character between the simple and the facet-eye, and has been termed a pseudo-facetted eye.—ED.]

* For the interpretation of these glands we refer the reader to p. 252.

The Alimentary Canal.

In treating of the formation of the alimentary canal, we must keep the Chilopoda and the Diplopoda quite distinct from each other. The accounts as yet given of the origin of the intestine in the Diplopoda, indeed, are by no means detailed, and do not throw sufficient light on the remarkable conditions which here appear to be presented to us.

The Enteron.

Chilopoda. The nutritive yolk upon which the germ-band lies is very large in *Geophilus*, and the yolk-pyramids are retained for some time (Fig. 112 *A*, *d*). In it lie the nuclei, which are assumed to have remained from the first in the yolk. These nuclei become arranged into a regular peripheral layer, and gradually the yolk becomes differentiated round each of them to form cell-areas (Fig. 124). The demarcation of the cells thus arises, and the enteron is formed (Sograff). Whether this differentiation takes place in one definite direction, *i.e.*, from before backward, cannot be clearly made out from Sograff's description, but Fig. 124 plainly indicates a progressive development of the enteron from behind forward. The large bulk of the nutritive yolk still remains for some time lying

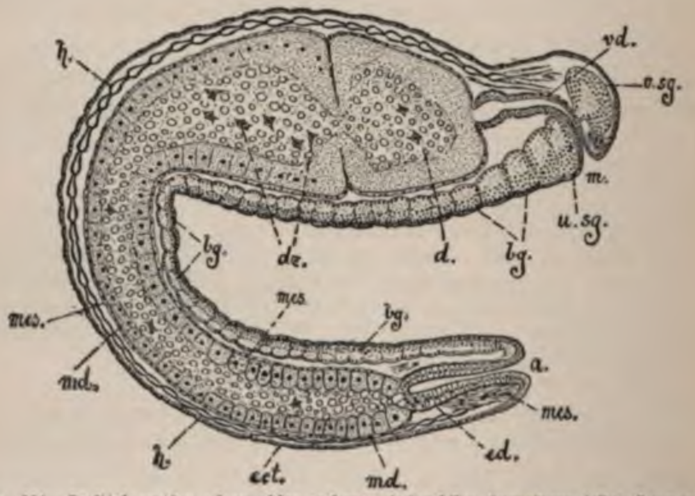

Fig. 124.– Sagittal section of an older embryo of *Geophilus ferrugineus* (after Sograff). *a*, anus; *bg*, ventral chain of ganglia; *d*, yolk; *dz*, yolk-cells; *ect*, ectoderm; *ed*, proctodaeum; *h*, heart; *m*, mouth; *md*, enteron, the development of which is not yet completed, the epithelium being still wanting anteriorly; *mes*, mesoderm, partly covering the intestine, partly distributed in the body-cavity; *o.sg*, supra-, *u.sg*, sub-oesophageal ganglion; *vd*, stomodaeum.

in the enteron, and is only gradually absorbed. It still serves as nourishment for the larva, and in *Lithobius* lasts for fifteen days after hatching.

Diplopoda. METSCHNIKOFF was the first to point out an important distinction in the formation of the enteron in the two chief divisions of the Myriopoda. In the Chilopoda it arises at the periphery of the yolk (Fig. 124), and thus surrounds the latter, while in the Diplopoda it forms as a tube within the yolk which thus comes to lie outside the gut (Fig. 125). In the Diplopoda also the enteron arises from the cells contained in the yolk, whose origin is as little known here as in the Chilopoda. They collect in a definite region, and become arranged so as to form a large tube extending along the longitudinal axis of the embryo (Fig. 125, *md*). This tube, which, in the figure taken from HEATHCOTE'S drawings, appears as a solid strand, lies, according to the unanimous accounts of METSCHNIKOFF and HEATHCOTE, within the yolk-mass, from which the first-named of these authors was able to remove it entire. The yolk itself thus comes to lie in the primary body-cavity, which it completely fills, penetrating, for example, into the spaces left on the separation of the ganglion-rudiments from the ectoderm (Fig. 126 *A* and *B*), and even apparently (HEATHCOTE) pressing in between the mesoderm-layer and the ectoderm (Fig. 126). The chain of ganglia thus lies within the yolk-mass, and the same is the case with the stomodaeum and proctodaeum, as is evident from Figs. 125 and 126 *B*. In later stages the yolk is taken up into the spaces of the pseudocoele, and there gradually absorbed (p. 250).

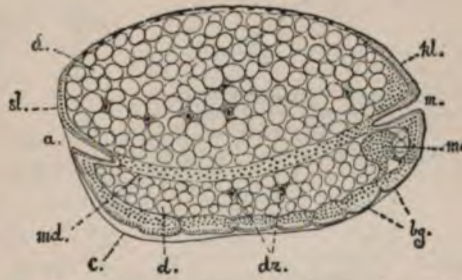

FIG. 125.—Longitudinal section through an embryo of *Julus terrestris* on the tenth day of development (after HEATHCOTE). *a*, anus; *bg*, ventral chain of ganglia; *c*, cuticular envelope of the embryo; *d*, yolk; *dz*, yolk-cells; *kl*, cephalic lobe; *m*, mouth; *md*, enteron; *mes*, mesoderm; *sl*, caudal lobe.

The presence of yolk in the primary body-cavity has already been mentioned in connection with *Moina* and *Mysis* (Vol. ii., p. 177), although in these cases it takes place somewhat differently. It may also occur, though on a much smaller scale, in the Insecta, as will be described later.

The difference in the formation of the enteron in the Chilopoda and in the Diplopoda is very striking, and can best be seen by a comparison of Figs. 124 and 125. While its formation in the Chilopoda recalls the conditions found prevailing in the Arachnida, in the Diplopoda its origin may be compared with certain phenomena in the Crustacea, in which the epithelium also at first lies within the yolk until this latter filters through into the rudiment of the intestine. Before these points can be judged with any certainty, further details as to the later relations of the enteron to the nutritive yolk must be ascertained. For the present the whole subject is obscure.

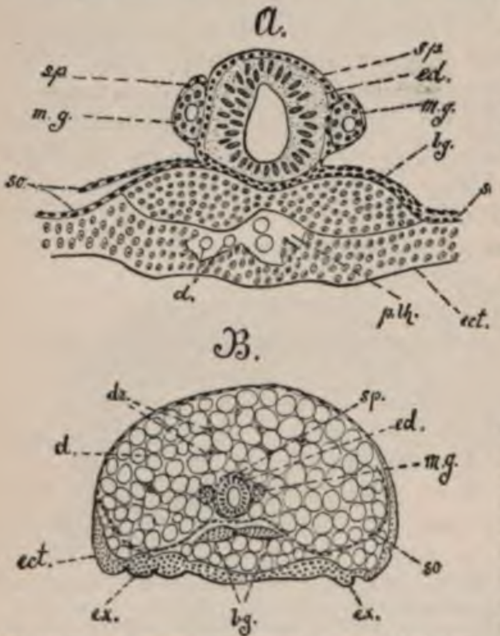

FIG. 126.—Transverse sections through embryos of *Julus terrestris* (somewhat diagrammatic, after HEATHCOTE). *A*, the ventral part of a transverse section through an embryo on the eleventh day. *B*, complete transverse section of an embryo on the twelfth day. Both sections are made through the posterior region of the body. *bg*, ventral ganglia; *d*, yolk; *dz*, yolk-cells; *ed*, proctodaeum; *ect*, ectoderm; *ex*, rudiments of limbs; *m.g*, Malpighian vessels; *p.lh*, primary body-cavity; *so*, somatic, *sp*, splanchnic layer of the mesoderm.

The Stomodaeum and the Proctodaeum.

The formation of the oesophagus and the rectum takes place in somewhat the same manner in the Chilopoda and the Diplopoda. Both these structures are ectodermal invaginations. The *stomodaeum* arises ventrally between the cephalic lobes, the *proctodaeum* also lies ventrally near the posterior end (Fig. 125, *m* and *a*). Each lengthens, the former posteriorly, the latter anteriorly, and they finally join the enteron, with the epithelium of which their walls fuse (Figs. 115, 124, 125). As the embryo grows, the anus shifts from its former ventral position, and comes to lie further back (Figs. 110 to 112, pp. 224 and 225, and Fig. 124, *a*).

The *Malpighian vessels* arise as two caecal outgrowths of the proctodaeum. In *Geophilus* these apparently form very early (Fig. 111, *m.g*), but in *Julus* their rudiments appear only at the time of hatching (*i.e.*, when the egg-shell splits, on the twelfth day of development).

The Mesodermal Structures.

In *Julus* the mesoderm first appears as an inwardly projecting keel-shaped thickening of the blastoderm (Fig. 108, HEATHCOTE), whereas, in *Geophilus*, a unilaminar plate of cells extends as a thickening along the ventral side (SOGRAFF). This rudiment of the mesoderm is said to arise not only by the increase of the blastoderm-cells, but to a great extent also from cells which remained in the yolk, and now wander to the ventral surface. At first the mesoderm consists of a continuous layer of cells, but it soon becomes divided along the middle line into two mesoderm-bands. These become divided up transversely into consecutive thickenings corresponding to the future segments, the mesoderm connecting these thickenings being very slight. The formation of cavities then takes place in the thickenings by the separation of the cells from one another (HEATHCOTE); the primitive segments are thus formed and the somatic and splanchnic layers of the mesoderm appear.

FIG. 127.—Transverse section through a *Geophilus* embryo, the germ-band of which is rolled round the yolk. Above, the anterior, and below, the posterior part of the germ-band is cut through (after SOGRAFF). *at*, antenna; *bg*, ventral chain of ganglia; *d*, yolk; *dz*, yolk-cells; *h.us*, cavities of the primitive segments extending into the limbs; *mes*, somatic mesoderm (outer wall of the primitive segments); *o.sg*, supra-oesophageal ganglion; *vd*, stomodaeum.

SOGRAFF believes that the two mesoderm-bands arise in the way which has repeatedly been described in connection with the Insecta. He assumes that the unilaminar cell-plate, which in *Geophilus* lies below the ventral ectoderm, bends round dorsally at its lateral edge, and grows towards the middle line. In this way two contiguous layers are formed, and through their shifting apart the secondary body-cavity arises. KOWALEVSKY has made a similar statement in connection with *Hydrophilus*, but this has not been confirmed by more recent observers. A somewhat similar account is given by HEYMONS for *Phyllodromia*. The cells distributed in the yolk also, according to SOGRAFF, take part in the formation of the splanchnic layer by shifting to its periphery.

The primitive segments that appear correspond in number to the future body-segments, and it is an important fact that *for each of the segments bearing two pairs of legs in the Diplopoda, two pairs of primitive segments form*, so that these segments are thus again proved to be double segments (HEATHCOTE). The statement that *the primitive segments extend into the limbs and cause these latter to appear hollow* (Fig. 127, *h.us*) seems to be universally applicable among the Myriopoda. This feature recalls *Peripatus*, and a further resemblance to this latter form is found in the fact that even each of the antennae contains a large diverticulum of a segmental cavity (Fig. 127, *h.us* and *at*). The conclusions on this point in connection with *Peripatus* (p. 186) would therefore also apply to the Myriopoda. In any case the diverticula of the segmental cavities that extend into the limbs seem to be a primitive condition which is lost later, and, among the Insecta, is only retained in the lower forms (*e.g.*, Orthoptera, GRABER, CHOLODKOWSKY, HEYMONS, etc.).

The Body-cavity, the Blood-vascular System, the Fat-body, and the Musculature.

The stage in which the mesoderm is represented by two rows of consecutive primitive segments does not last long. According to HEATHCOTE each primitive segment divides into two vesicles, one of which remains in the body (somatic part of the coelom), while the other lies in the limb (pedal or crural part of the coelom), a condition which may be compared with the similar distribution of the primitive segments in *Peripatus*.

There are certain differences in detail in the further development of these two parts of the primitive segments in *Peripatus* and in the Myriopoda, but this subject, in spite of HEATHCOTE's observations, is still somewhat obscure, and a more detailed study of it is very desirable.

In tracing the development of the primitive segments from before backward, we find that the first segment, the pedal section of which lies in the antennae, is used chiefly for the formation of the antennal musculature and for the musculature of the head generally. The primitive segments of the mandibles are in the same way concerned in the formation of musculature, but those of the maxillary segment have, according to HEATHCOTE, another significance (formation of the salivary glands), which will be discussed below.

From the first trunk-segment onward, the two sections of the coelom show throughout a difference in their ultimate development. While the pedal coelomic sacs are used for the development of the leg-musculature and lose their sac-like form, the somatic parts, in the Diplopoda, shift towards the middle line and come to lie above the ventral chain of ganglia and here later fuse with one another. They thus differ from the corresponding parts in *Peripatus*, which shift dorsally and come into contact above the intestine (p. 208 and Fig. 102, p. 205). Here, however, as there, they form the genital glands, and since, in the Chilopoda, these lie dorsally to the intestine, we might expect in these forms greater agreement with the arrangement in *Peripatus* than is found in the Diplopoda.

During the differentiation of the two sections of the primitive segments just described, connected layers of cells seem to be formed, and these become arranged above the chain of ganglia and round the intestine (Fig. 126, *so* and *sp*), at least **Heathcote** mentions a covering of these parts which he designates (though not quite correctly) as the somatic and the splanchnic mesoderm. The actual body-cavity is a pseudocoele, and its condition is thus quite peculiar, since, as already shown (p. 245), the largest part of the yolk lies outside of the enteron and consequently in the body-cavity (Figs. 125 and 126 *B*, pp. 245 and 246). Cells still remain in the yolk, and these have been considered as of great importance in the development of the blood-vascular system as well as the fat-body and the connective tissue (**Sograff**, **Heathcote**).

As has already been mentioned, the cell-material derived from the primitive segments co-operates in the formation of the tissues bounding the body-cavity and especially of the musculature. It is evident, from Fig. 126 *A* and *B*, that a layer of mesoderm-cells (*so*) becomes closely applied at first to the ventral ectoderm and to the ganglionic chain, but later this layer becomes detached from the outer layer; both it and the nerve-cord shift into the yolk. During these processes, which are not yet satisfactorily worked out, small particles of yolk seem in some way to press in between these parts and the ectoderm (Fig. 126 *A* and *B*, *d*). On the other hand, it no doubt results that the mesodermal elements derived from the primitive segments also become distributed in the yolk, and consequently the organs which develop here are not to be derived solely from the cell-elements which remained in the yolk.

In the Chilopoda, the enteric epithelium forms at the periphery of the yolk, which thus comes to lie within the intestine. We should be inclined to believe that in this case the mesodermal tissue would be derivable from the primitive segments, and yet **Sograff** assumes that in the lateral parts of the embryo, as well as on the back, to which the primitive segments have not extended, a parenchymatous tissue consisting of star-like cells appears derived from the cells which remained in the yolk.* These were said before to take part in the formation of the splanchnic layer (which arose principally by the bending over of the cell-plate first present) by shifting from the yolk to the periphery. In the same way we must assume, according to **Sograff**, that wandering cells come out of the yolk later, though before the enteric epithelium has formed, to yield the parenchymatous tissue. From this latter the connective tissue of the body-cavity, the fat-body, and the blood-corpuscles are said to be derived.

In the Diplopoda, the connective tissue of the body-cavity, the fat-body, and the blood-corpuscles arise from the cells already lying with the yolk in the body-cavity. The yolk-mass in this last case becomes more and more interpenetrated with cells; the yolk itself seems to remain in the cavities of the pseudocoele, and here to be

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* We believe that the above is a correct reproduction of **Sograff**'s view, although it is difficult to obtain from his Russian treatise a complete conception of these somewhat complicated formative processes.

gradually absorbed. It can still be traced in the cellular network in the form of somewhat large structures resembling oil drops, which represent the fat-body of the larva. With the gradual absorption of the yolk and the simultaneous further development of the mesodermal elements, the primary body-cavity of the Diplopoda (Figs. 125 and 126 *B*), formerly filled with the compact mass of yolk, passes at first into a pseudocoele formed of a cellular network, and finally into the definitive body-cavity.

The formation of the body-cavity in the Diplopoda seems to resemble that in *Moina*. In this form also the food-yolk lies in the primary body-cavity (Vol. ii., p. 177). Cells which become detached from the mesoderm-bands are disseminated through it, and consequently these must indisputably be considered as true mesoderm-cells. These cells later also assist in the formation of the blood-tissue. A similar fate is probably reserved for the yolk-particles remaining in the pseudocoele of the *Muscidae*.

The formation of the heart in the Diplopoda is said also to be traceable to the cells contained in the yolk (?). These become arranged in the pseudocoele to form a dorsal tube, which at first is incompletely closed, but later becomes complete. Regularly-placed paired apertures that are retained in this tube represent the ostia. In each double segment of the Diplopoda two pairs of ostia develop. In the same way, each double segment possesses two pairs of arteries, which leave the heart ventrally and run direct into

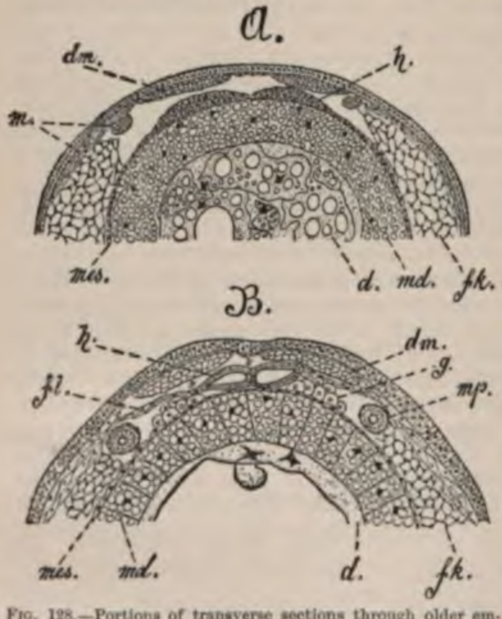

FIG. 128.—Portions of transverse sections through older embryos of *Geophilus ferrugineus* (after SOGRAFF). The sections are made through the posterior part of the body. *d*, yolk-mass with yolk-cells; *dm*, dorsal muscles; *fk*, the fat-body; *fl*, alary muscles of the heart; *g*, rudiment of the genital glands; *h*, the paired rudiment of the heart; *m*, musculature; *md*, enteron; *mes*, mesodermal covering of the intestine; *mp*, Malpighian vessels.

the cavities of the pseudocoele. Ventrally to the heart a pericardial septum forms, which has the same origin as the heart itself (HEATHCOTE).

According to SOGRAFF, the heart of *Geophilus* arises from a series of paired cell-accumulations lying on the already formed intestine (Fig. 128 *A*). When it is said that these belong to the splanchnic layer, the splanchnic layer proper of the primitive segment can hardly be intended, but rather one of the coverings of the intestine derived from the parenchymatous tissue. This is the sense in which HEATHCOTE also speaks of a splanchnic and a somatic layer (Fig. 126, *sp* and *so*). In the cell-accumulations, each pair of which corresponds to one of the chambers of the adult heart and to a body-segment, cavities appear (Fig. 128 *B*). The two sacs belonging to each pair fuse together, uniting in the middle line, and thus form a chamber of the heart, and the consecutive chambers, uniting together, form the whole dorsal vessel (Fig. 124). The heart in its development closely resembles the dorsal vessel of the Annelida which is derived from paired rudiments (Vol. i., p. 291), and, if this account of its origin prove correct, the Chilopoda would appear to show in this respect a still more primitive condition than is found even in *Peripatus*.

The body-musculature arises out of the mesodermal elements which become applied to the ectodermal body-wall, but, as we said before, nothing certain is known of the derivation of these elements.

The Salivary Glands.

Although one cannot but be predisposed to homologise the salivary glands of the Myriopoda with those of the Insecta, and therefore to regard them as ectodermal structures, we are compelled by HEATHCOTE's statements to consider them as mesodermal. The salivary glands are said by him to be formed as tubular outgrowths of the somatic portion of the primitive somite of the maxillary segment, *i.e.*, the inner division of the primitive segment (p. 248). When the tube has grown to some length it opens externally by fusing with the ectoderm on each side at the base of the maxillary plate.

Should the origin of the salivary glands out of the mesoderm actually be confirmed, we should have to regard them as transformed nephridia, whereas the salivary glands of the Insecta, in consequence of their ectodermal origin, must no doubt be considered as crural glands. The salivary glands of the Myriopoda would then be formed in the same way as those of *Peripatus* (p. 206), although in the latter it is the lateral not the inner portion of the primitive segment that gives rise to them. The question as to the direct homology of the salivary glands in the Myriopoda and *Peripatus*, is identified with that of the homology of the mouth-parts in the two groups. These glands, in *Peripatus*, belong to the segment of the oral papillae, and the question of the co-relation of these appendages to the mouth-parts of the Myriopoda will be discussed at the end of this volume.

In itself, the origin of the salivary glands out of the mesoderm does not appear to us very probable. The Myriopoda, moreover, possess several pairs of these glands (HERBST, No. 9) occurring in the individual cephalic segments, just as the pairs of salivary glands in the Insecta are distributed on the segments of the mandibles, the maxillae and the lower lip. Nothing appears more likely than that the structures in the Insecta and in the Myriopoda are homologous. It is indeed possible that, as in *Peripatus*, glands of mesodermal origin may occur side by side with those of ectodermal origin. It would therefore be of primary importance to establish accurately the manner of development of these glands.

If the salivary or cephalic glands (HERBST applies these two names indifferently to them since spinning glands also are found among them) are of ectodermal nature, they would have to be regarded as crural glands. Such glands (probably ectodermal) are also often found on the trunk in the Myriopoda, and have been compared to the crural glands of *Peripatus*, and further, to the parapodial glands of the Annelida. In the Myriopoda these glands vary greatly in character. They are described in detail by EISIG (No. 2), who is disposed to regard the protective glands which were described above, according to the accounts of METSCHNIKOFF and HEATHCOTE, as ectodermal, as transformed nephridia.

The Genital Organs.

The little that is as yet known as to the formation of the genital organs relates to the genital glands of the Diplopoda. These, as in *Peripatus*, proceed from the somatic or inner part of the primitive segments, which, however, is not, as in *Peripatus*, shifted towards the dorsal side, but remains in a ventral position. A large number of primitive segments is used in the formation of the genital glands. The somatic part of these segments shifts towards the median line and comes to lie above the ventral chain of ganglia. The coelomic sacs of the right and left side of each segment come into contact in the middle line. About the time when the embryo hatches, the two fuse so that a single cavity results, and as the consecutive coelomic sacs also unite, a long tube is formed lying between the ventral chain of ganglia and the intestine. This is the genital tube.

We have no altogether reliable accounts of the relation of the genital tube to the efferent ducts. In *Peripatus*, the efferent ducts are known to correspond to a pair of nephridia and open out posteriorly. In the Myriopoda, a special interest attaches to this question, because the genital organs in the Chilopoda open posteriorly (on the penultimate segment), in the Diplopoda, on the other hand, somewhat far forward (behind the second pair of legs). We are inclined to regard the arrangement in the Chilopoda as the more primitive, and to assume a secondary displacement of the efferent ducts in the Diplopoda, a process which can best be explained through the utilisation of another pair of nephridia. A displacement of the genital aperture by the occurrence of an additional segment behind this, the penultimate segment, and by the disappearance of anterior segments seems altogether improbable.

The position of the genital glands themselves appears to us more primitive in the Chilopoda than in the Diplopoda, and like that of their efferent ducts, more nearly to correspond to the condition in *Peripatus.* The glands lie dorsally to the intestine, and in the embryo appear as two accumulations of cells near the dorsal vessel (Fig. 128 *B*, *g*). Their origin is, unfortunately, as yet obscure.

[An important contribution to the ontogeny of the Chilopoda has recently been made by HEYMONS (No. III.). This author has entirely reinvestigated the development of *Scolopendra*, but unfortunately so far has only published a short summary of his results. He finds that the egg possesses a central unsegmented yolk containing segmentation-nuclei; some of the latter migrate to the surface and form the blastoderm, while others remain within the yolk and give rise to some yolk-cells. The yolk-cells also arise as immigrants from all parts of the blastoderm, as also do the entoderm-cells. There is no gastrula-groove. The body is found to consist of the following segments:—a primary cephalic plate and a primary anal piece (telson), between which are found (1) an antennular, (2) an antennal, (3) an intercalary, (4) a mandibular, (5, 6) two maxillary, (7) a maxillipedal, (8–28) the body-, and (29, 30) the genital segments. The salivary glands are purely ectodermal and not modified nephridia. A coelomic cavity is present in each segment, cephalic plate and telson excepted, in all thirty pairs. The unpaired gonad and genital duct of the adult are paired in the embryo, and arise in connection with the coelom; as in the Insecta, the ducts have ectodermal terminations with accessory glands. For the brain, see footnote, p. 241. HEYMONS concludes that the Chilopoda show close relationship to the Hexapoda and are very remote from the Diplopoda, the Myriopoda not forming a natural group.—ED.]

General Considerations.

In considering the ontogeny of the Myriopoda, two important questions arise—(1) whether the developmental history of the Myriopoda testifies to their near relationship to *Peripatus*, and (2) in what way their ontogeny is related to that of the Insects. Since the Myriopoda appear in a certain sense as intermediate forms between the Insecta and the Onychophora, these questions naturally suggest themselves. It must at once be stated that up to the present time the ontogeny of the Myriopoda is too little known to enable us to answer these questions in a manner as satisfactory as might be desired.

Even with regard to the first ontogenetic processes in the Myriopodan egg, we must hesitate in instituting a comparison with *Peripatus.* A superficial cleavage accompanied by segmentation of the yolk takes place in the eggs of the Myriopoda, and the same kind of cleavage has been affirmed of the egg of *Peripatus novaezealandiae*, which is rich in yolk (Fig. 76 *A*, p. 167). The eggs of other species of *Peripatus* undergo total cleavage as has been seen, but this method of cleavage was regarded as probably secondary. Further, it is of interest in this connection that the eggs of the lowest Insects (*Podura*) are also said to undergo total cleavage, although we are still without certainty on this point.

The formation of the germ-layers in the Myriopoda is still too little understood for us to draw definite conclusions from it, but the external form of the body offers a few points of comparison, though these are perhaps not very certain. It was shown that the Myriopodan egg undergoes a decided ventral folding at an early stage of development, and that this may lead to the sinking of the whole germ-band into the yolk (Figs. 113–116, pp. 226–230). This also appears to be the case in *Peripatus*, judging from the statements and drawings of L. **Sheldon**, and it seems not impossible that these developmental processes which occur in the Myriopoda and the Insecta are foreshadowed in *Peripatus*.*

Indications of a low grade of development, and at the same time of resemblance to *Peripatus*, are afforded by the suggestion of ventral organs (of head and trunk), the continuation of the primitive segments into the extremities, especially into the antennae, the condition of the ectodermal (crural) glands and of the salivary glands (which perhaps arise from the mesoderm), also by the double rudiment of the heart and by the formation of the genital glands; but unfortunately our knowledge of the ontogenetic processes in these cases is not sufficient to raise conjecture to the level of certainty. The adult animal is better understood, and in it the constitution of the mouth-parts, the segmentation of the nervous system, the structure of the eyes, the presence of the Malpighian vessels, as well as the condition of the blood-vascular system and the body-cavity prove without doubt the near relationship of the Myriopoda to the Insecta. By far the most striking point of agreement is afforded by the tracheae, which are constituted exactly like those of the Insecta. If we now ascribe great importance to a point which was not considered applicable in a comparison with the Arachnida, it is because a derivation of the long and fairly homonomously segmented Myriopoda from forms like *Peripatus* already provided with tracheae is naturally suggested, while such a derivation of the Arachnida is met with great difficulty, as has already been shown more in detail (p. 110).

In spite of the great agreement existing between the tracheal system of the Myriopoda and that of the Insecta in the adult stage, one fact in connection with the former seems to suggest

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* [See footnote, p. 216.—Ed.]

the condition found in *Peripatus*. The tracheae in the Myriopoda, as in *Peripatus*, appear very late; they are said to form only during post-embryonic life, whereas in the Insecta they appear as rudiments in an earlier stage of development.

At first sight, the occurrence of larval forms provided with comparatively few segments and still fewer pairs of limbs might seem to be a fact of great significance, all the more that these closely resemble in appearance the young forms of the lowest Insects, viz., the Thysanura. This brings us to the question whether the rich segmentation of the Myriopodan body represents on the whole a primitive condition, or whether it is a secondarily acquired character. We might answer that the racial form of the Myriopoda was a homonomously segmented form, consisting like *Peripatus* of a large number of segments, or we might, with HAASE (No. 5) assume that the large number of segments such as are now found in the Myriopoda represents a later acquisition by these forms. The continuous lengthening of the body has been explained by the manner of life of the Myriopoda, which is accompanied by such a development of the body in the same way as in the Serpents among Vertebrates. It is interesting to see how this lengthening of the body leads to a modification of its morphological characters. In those Chilopoda whose bodies consist of many segments, unpaired chitinous plates appear in the soft intersegmental ventral integument, which in the shorter Chilopoda is only slightly developed, and as the length and the number of the segments increase, these become broad ventral plates, the unpaired scuta (HAASE, No. 6).

The common primitive form of the Insecta and the Myriopoda has repeatedly been sought in some form approaching the Symphyla; but *Scolopendrella*, to which, on account of its striking resemblance to the Thysanura (Figs. 192 and 193), this great significance was attached, shows as well as the latter certain peculiarities of organisation which prevent it as much as the Thysanura from being regarded as a primitive form. We do not indeed doubt that the Symphyla as well as the Thysanura are very ancient forms, but we would assume a racial form for the Myriopoda with still more primitive organisation, the Symphyla being somewhat removed from that form and the Thysanura still further. The differentiation of a thorax, which is an important character of the latter, but which is merely indicated in the Myriopoda, will be discussed in dealing with the Insecta.

The Diplopoda resemble most insect larvae in leaving the egg at a stage with few segments and with only three well developed pairs of legs. The Chilopoda when hatched always have a large number of segments and pairs of legs, some even possessing the full adult number. We should feel inclined to consider this as the more primitive condition, especially as *Peripatus* also possesses the full number of segments when hatched, did not the whole organisation make it appear doubtful which of the two divisions, the Chilopoda or the Diplopoda, is the more primitive.

The invagination of the embryo, or ventral flexure of the germ-band of the Chilopoda, as well as their further development, seems to take place in a primitive way, as it appears to be merely a consequence of increase in length, while the early bending of the germ-band of the Diplopoda does not admit of such a natural explanation, but must rather be regarded as a derived condition. On the other hand, the cylindrical form of the Diplopodan body seems to represent a more primitive condition, since the Chilopodan embryo also is cylindrical and becomes flattened dorso-ventrally only after hatching.

Whereas, in the Chilopoda, each body-segment carries a pair of limbs, in the Diplopoda we see every two segments fusing together to form one, which is then provided with two pairs of limbs. Ontogeny has shown that for every segment of the Diplopoda, two primitive segments and two ganglia appear as rudiments; the double nature of these segments can thus no longer be questioned. In this we certainly have a secondary character in the Diplopoda. The mouth-parts of this division, nevertheless, are far simpler than those of the Chilopoda, in that the former probably possess only one pair of maxillae, while in the Chilopoda two more pairs of extremities are drawn in to assist this pair in the work of mastication. The tracheal system is simpler in the Diplopoda and more complicated in the Chilopoda, but, on the other hand, a more primitive condition of the genital organs is found in the latter, the genital glands first appearing dorsally to the intestine (as in *Peripatus*) and retaining this position, while in the Diplopoda they are found ventrally to the intestine. In the former, the genital aperture belongs to the penultimate body-segment, whereas, in the latter, it lies near the anterior end of the body, between the second and third trunk-segments. It can hardly be doubted that the position of the genital aperture at the posterior end of the body represents the primitive condition, and that in other cases that condition has been modified.

When it is further added that the Diplopoda appear palaeontologically as the older, and the Chilopoda as the younger forms, it only remains to be said that the latter also became separated from the racial form early, and each branch, developing further independently, while retaining ancient features, acquired characters which, in consequence of their separate development, were not the same in the two groups.

The most important feature in the organisation of the Myriopoda is the uniform development of the trunk-segments and the possession of limbs on all or nearly all these segments. This feature gives the Myriopoda a specially primitive character, and brings them near to those other forms which show a homonomous segmentation of the body, viz., *Peripatus* and the Annelida.

[In the above account the Myriopoda are treated as a natural group, and as such they are probably regarded by the majority of zoologists. This, however, is not the opinion of those who have specialised in this group, and a separation of the Diplopoda from the Chilopoda was suggested as early as 1887 by Pocock, a view which he afterwards amplified (No. VI.). Pocock regards the Chilopoda with the Symphyla as much more nearly related to the Hexapoda than to the Diplopoda with the Pauropoda, and he proposes to divide the Tracheata into two groups—(1) the Opisthogoneata, including the Hexapoda, Chilopoda, and Symphyla; and (2) the Progoneata, embracing the Diplopoda and the Pauropoda, the latter, according to Kenyon, being modified Diplopods. He regards the Symphyla as standing nearest the ancestral form of the whole group. Precisely similar conclusions have been arrived at by Silvestri (No. IX.), who also has made a special study of the Myriopoda. These views have been accepted by Ray Lankester (No. V.) and others. Kingsley (No. IV.), while agreeing that the Myriopoda form a purely artificial group and that the Chilopoda are closely related to the Hexapoda, differs from Pocock in concluding that the Diplopoda have probably no relation at all to the Chilopoda. The view that these two subdivisions of the Myriopoda are quite distinct from one another, or at the most but slightly related, is amply confirmed by the study of their ontogeny, as may be seen from the numerous points of difference mentioned above.—Ed.]

LITERATURE.

1. Bode, J. Polyxenus lagurus. Ein Beitrag zur Anatomie, Morphologie u. Entwicklungsgeschichte der Chilognathen. *Zeitschr. f. d. ges. Naturwiss.* Bd. xlix. *Halle*, 1877.
2. Eisig, H. Die Capitelliden. *Monographie der Fauna u. Flora des Golfes von Neapel.* xvi. *Berlin*, 1887.
3. Fabre, L. Recherches sur l'anatomie des organes reproducteurs et sur le développement des Myriopodes. *Ann. Sci. Nat.* (4). Tom. iii. *Paris*, 1855.
4. Grenacher, H. Ueber die Augen einiger Myriapoden. *Archiv. f. Mikro. Anat.* Bd. xviii. 1880.
5. Haase, E. Beitrag zur Ontogenie u. Phylogenie der Chilopoden. *Zeitschr. f. Entomologie.* N. F. Heft viii. *Breslau*, 1881.

6. Haase, E. Die Abdominalanhänge der Insekten mit Berücksichtigung der Myriopoden. *Morph. Jahrb.* Bd. xv. 1889.

7. Heathcote, F. G. The early development of Julus terrestris. *Quart. Journ. Micro. Sci.* Vol. xxvi. 1886.

8. Heathcote, F. G. The post-embryonic development of Julus terrestris. *Phil. Trans. Roy. Soc. London.* Vol. clxxix. 1888.

9. Herbst, C. Anatomische Untersuchungen an Scutigera coleoptrata. *Dissertation. Jena,* 1889.

10. Latzel, R. Die Myriopoden der Oesterreich-Ungarischen Monarchie. *Wien,* 1880 and 1884.

11. Metschnikoff, E. Embryologie der doppeltfüssigen Myriopoden (Chilognatha). *Zeitschr. f. Wiss. Zool.* Bd. xxiv. 1874.

12. Metschnikoff, E. Embryologisches über Geophilus. *Zeitschr. f. Wiss. Zool.* Bd. xxv. 1875.

13. Newport, G. On the organs of reproduction and the development of the Myriopoda. *Phil. Trans. Roy. Soc. London.* 1841.

14. Packard, A. S. On the Morphology of the Myriopoda. *Proc. Amer. Phil. Soc. Philadelphia.* Vol. xxi. 1884. Also in *Ann. Mag. Nat. Hist.* (5). Vol. xii.

15. Rath, O. vom. Beiträge zur Kenntniss der Chilognathen. *Inaug.-Dissertation. Bonn,* 1886.

16. Rath, O. vom. Ueber die Fortpflanzung der Diplopoden (Chilognathen). *Ber. d. Naturforsch.-Gesellsch. Freiburg i. Br.* Bd. v. 1891.

17. Rath, O. vom. Zur Biologie der Diplopoden. *Ber. d. Naturforsch.-Gesellsch. Freiburg i. Br.* Bd. v. 1891.

18. Saint Remy, G. Contributions à l'étude du cerveau chez les Arthropodes trachéates. *Archiv. Zool. Expér.* (2). Tom. v. Suppl. 1887–1890.

19. Sograff, N. Zur Embryologie der Chilopoden. *Zool. Anz.* Jahrg. v. 1882.

20. Sograff, N. On the embryonic development of Geophilus ferrugineus and G. proximus. (Russian). *Izvyest. Imp. Obshch. Lyub. Estestv. Antrop. i Ethnog. Moscow.* Tom. xliii. 1883. (Abstracted in *Zool. Jahresb. d. Stat. Neapel.* 1883.)

21. Stecker, A. Die Anlage der Keimblätter bei den Diplopoden. *Arch. f. Mikro. Anat.* Bd. xiv. 1877.

22. **Tömösvary, E.** Eigenthümliche Sinnesorgane der Myriopoden. *Math. Naturwiss. Berichte aus Ungarn.* Bd. i. *Pest* and *Berlin*, 1882-83.

APPENDIX TO LITERATURE ON MYRIOPODA.

I. **Adensamer, T.** Zur Kenntniss der Anatomie und Histologie von Scutigera coleoptrata. *Verh. Z. Bot. Ges. Wien.* Bd. xliii. Ueber das Auge von Scutigera coleoptrata. *Sitzungsber. Z. Bot. Ges. Wien.* Bd. xliii. 1893.

II. **Cholodkovsky, N. A.** Zur Embryologie der Diplopoden. *C. R. Soc. St. Petersburgh.* 1895. (Printed in Russian. Résumé in German.)

III. **Heymons, R.** Zur Entwicklungsgeschichte der Chilopoden. *Sitzungsber. k. preuss. Akad. Wiss.* 1898.

IV. **Kingsley, J. S.** The classification of the Arthropoda. *Amer. Nat.* 1894.

V. **Lankester, E. Ray.** Are the Arthropoda a Natural Group? *Nat. Sci.* 1897.

VI. **Pocock, R. I.** On the classification of the Tracheate Arthropoda. *Zool. Anz.* Jahrg. xvi. 1893.

VII. **Rosenstadt, B.** Zur Morphologischen Beurtheilung der Augen von Scutigera. *Zool. Anz.* Jahrg. xix. 1896.

VIII. **Schmidt, P.** Beitrage zur Kenntniss der niederen Myriapoden. *Zeitschr. f. Wiss. Zool.* Bd. lix. 1895.

IX. **Silvestri, F.** I. Diplopodi. Part i. Sistematica. *Ann. Mus. Civ. Genova* (2a). xvi. 1896.

X. **Verhoeff, C.** Zur Phylogenie der Myriapoden-Ordnungen. (Two papers.) *Zool. Anz.* Jahrg. xix. 1896.

XI. **Willem, V.** Les ocelles de Lithobius et Polyxenus. *Bull. Soc. Mal. Belg.* Tom. xxvii.

CHAPTER XXVII.

INSECTA.

Systematic (after Brauer, No. 146):—

A. Apterygogenea.
  - *a*. Thysanura (*Campodea, Japyx, Machilis, Lepisma*).
  - *b*. Collembola (*Podura, Sminthurus*).

B. Pterygogenea.
  - *a*. Dermaptera (*Forficula*).
  - *b*. Ephemeridae.
  - *c*. Odonata (*Libellulidae*).
  - *d*. Plecoptera (*Perlidae*).
  - *e*. Orthoptera genuina (*Blattidae, Phasmidae, Mantidae, Saltatoria*).
  - *f*. Corrodentia (*Termitidae, Psocidae, Mallophaga*).
  - *g*. Thysanoptera (*Physapoda, Thrips*).
  - *h*. Rhynchota.

  } Homomorpha.

  - *i*. Neuroptera (*Sialidae, Megaloptera*).
  - *k*. Panorpatae.
  - *l*. Trichoptera (*Phryganea*).
  - *m*. Lepidoptera.
  - *n*. Diptera.
  - *o*. Siphonaptera.
  - *p*. Coleoptera.
  - *q*. Hymenoptera.

  } Heteromorpha.

I. Embryonic Development.

1. Oviposition and the structure of the ripe egg.

Most Insects are oviparous, only a few forms bringing forth their young alive, *e.g.*, the parthenogenetic generations of the *Aphidae*, many Diptera (*Sarcophaga, Tachina, Oestridae, Pupipara, Cecidomyia* larvae), the *Stylopidae*, and a few Coleoptera (many *Staphylinidae*). The eggs when laid are protected from external injuries in many different ways, either by being glued to some surface or by being deposited in water, below ground, or within the tissues of plants. In the last case the laying of the eggs often gives rise to excrescences on the plants (galls). Insects whose larvae live as parasites in the body-cavity of other Insects (*Ichneumonidae*) lay their eggs in the body of the future host within which the embryonic and post-embryonic development take place. Many Insects surround their eggs with a web, others envelop them in a secretion which, in the case of eggs laid in water, swells up as a jelly (spawn of the *Culicidae* and *Phryganeidae*), but in other cases hardens into a firm capsule by exposure to the air (so-called egg-case or cocoon of *Periplaneta* and *Mantis*), etc.

The eggs of Insects are usually distinguished for their large size. They show great variety of form, the most prevalent being an elongate oval, the long axis of the egg corresponding with the future long axis of the larva. In such eggs a distinction between the future dorsal and ventral surfaces is indicated by a difference in curvature (Fig. 129, *d* and *v*).

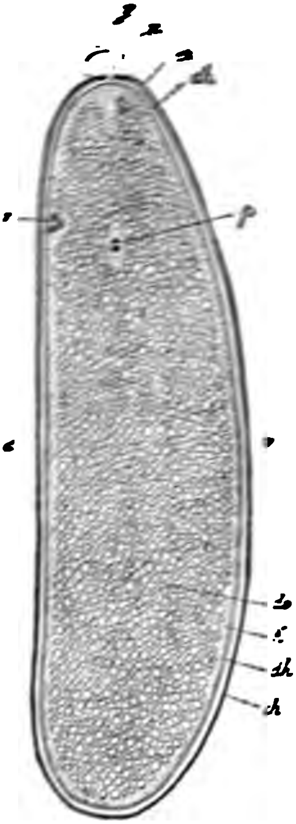
The mature egg is enclosed within two envelopes, an inner *vitelline membrane* (Fig. 129, *dh*) secreted by the egg itself, and an outer *chorion* (*ch*) secreted by the epithelium of the ovarian tube. The latter occasionally breaks up into two layers, the endochorion and the exochorion. The vitelline membrane is usually a homogeneous delicate structureless membrane, but the chorion is seldom thus constituted. In most cases it is ornamented by the presence of a network of thickened ridges and markings, which vary greatly in the different genera and species.

The chorion is pierced at one or more points (*micropyles*, Fig. 129, *m*) to allow of the passage of the spermatozoa, and the modification of the chorion that takes place round these micropyles often results in a very complicated micropylar apparatus, round which the vitelline membrane appears attached to the chorion (Fig. 129), so that both membranes appear perforated at this point.

In Insect eggs there is always a distinction between an anterior and a posterior pole. The anterior pole is that which, in the body of the mother, lay directed towards the head, and thus corresponded to the upper end of the ovarian tube. In later stages of embryonic development, the head end of the embryo always lies at this pole, while the posterior end of the embryo is directed towards the posterior pole of the egg. The micropylar apparatus usually lies at the anterior pole of the egg.

A cap of glutinous matter often covers the micropyle-area (Fig. 129, *g*), and may extend as an envelope over the greater part, or even the whole of the egg.

In the egg itself there is usually a separation of a superficial layer consisting of formative protoplasm (Fig. 129, *K*) from an inner mass [illegible] The peripheral layer of [illegible] "Keimhautblastem" of Weismann [illegible] has been found wanting in a few cases. [illegible] is usually quite thin and inconsiderable when compared with the amount of the central food-yolk. It might almost be thought to be disappearing. Only the eggs of certain small Insects are found to be comparatively poor in yolk. Some of these are forms in which the larva which emerges from the egg is distinguished by its small size (Aphides), or in which the nourishment of the embryo is provided for in some other way, either by its development within the body of the mother (viviparous Aphides), or by the embryo passing through its development endoparasitically in the coelomic fluid of some other Insect (Ichneumonidae). In all these forms the poverty in yolk has a determining influence on the course of embryonic development as will be seen later. These modifications are probably secondary, and an ovum well provided with food-yolk is no doubt to be regarded as the primitive type of Insect egg.



[illegible] food-yolk [illegible] cap over the micropyle; [illegible] peripheral protoplasm (periplasm) [illegible] micropyle; [illegible] male and female pronuclei before [illegible] polar bodies; [illegible] ventral side of the egg.

The central yolk-mass in the Insect egg (*do*) consists of a fine network of formative protoplasm, within the meshes of which the numerous particles of food-yolk and spherical fat-drops are contained. The elements of the food-yolk appear as strongly refractive bodies which are spherical or polygonally flattened by mutual pressure, and apparently structureless and homogeneous.

The germ vesicle of the maturing insect egg lies in the central part of the yolk, and appears as a large vesicular nucleus provided with a delicate chromatine network. During the process of maturation it shifts to the surface of the egg, there a spindle is formed, and the nucleus undergoes division. In this way the first, and afterwards the second, polar body is formed (BLOCHMANN, No. 5).

The position of the polar spindle varies in the different groups of the Insecta. In some (*Pieris*) it lies directly at the anterior pole of the egg, but in most Insects it is formed nearer the middle of the long axis of the egg. BLOCHMANN (No. 5) found it in *Blatta* in the middle of the dorsal surface, while in *Musca* it occurs at about one-third to one-fourth of the whole length behind the anterior pole on the concave (dorsal) side of the egg (Fig. 129, *r*). In the *Formicidae* it also lies laterally, but near the anterior pole, while in the *Aphidae* it is situated at the middle of one of the lateral surfaces of the egg. In *Hydrophilus* (HEIDER) it lies somewhat behind the mid-lateral region.

2. Cleavage and the Formation of the Blastoderm.

The type of cleavage universally prevalent among the Insecta* is the pure superficial type so common among the Arthropoda (Vol. ii., (p. 113). The first cleavage-nucleus (produced in the fertilised egg by the union of the male and female pronuclei) shifts inward and increases by indirect nuclear division (Figs. 131 *A* and 175 *A*, *B*, *C*, *f*). The formation by division of the numerous cleavage-nuclei from the first has only been directly observed in those eggs that are poor in yolk (*Aphidae*, *Cecidomyia*, *Cynipidae*). But it can hardly be doubted that in the larger yolk-bearing eggs of other Insects the numerous cleavage-nuclei which are found distributed throughout the egg soon after it has been laid are actually produced from the first cleavage-nucleus by nuclear division. These numerous nuclei, with the star-like areas of protoplasm which surround them, represent the formative elements of the blastoderm. TICHOMIROFF has, however, conjectured in the case of the egg of *Bombyx*, and HENKING (No. 39) has more definitely maintained in the case of *Musca* that these nuclei in their protoplasmic islands distributed throughout the yolk-masses have been produced by free formation of nuclei.† But this view appears to us altogether untenable. It is contradicted by the observations of BLOCHMANN (No. 5), according to which all the cleavage-nuclei in *Musca* undergo

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* ULJANIN (No. 83) believes that total and equal cleavage occurs in the *Poduridae*. It appears, however, from the researches of LEMOINE that even here cleavage is superficial, and the same conclusion is arrived at by GRASSI (No. 33) from the condition of the food-yolk in the later stages in *Japyx*. [According to HENNEGUY (No. XII.), cleavage is total in the eggs of *Smicra*, one of the *Chalcididae*. This is obviously a derived condition, as these are parasitic forms and the egg is nourished at the expense of the host.—ED.]

† [HENKING (No. XI.) has since modified this statement. See also footnote p. 167.—ED.]

division simultaneously (Fig. 130 *C*), which indicates that they represent a generation of descendants of the first cleavage-nucleus, all being of the same age; and it is further disproved by the direct observations above mentioned as being made on some small eggs.

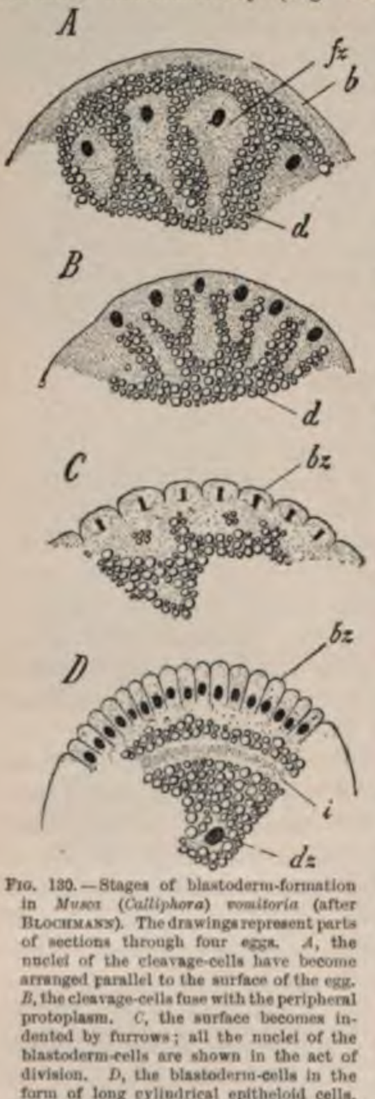

Fig. 130.—Stages of blastoderm-formation in *Musca* (*Calliphora*) *vomitoria* (after **Blochmann**). The drawings represent parts of sections through four eggs. *A*, the nuclei of the cleavage-cells have become arranged parallel to the surface of the egg. *B*, the cleavage-cells fuse with the peripheral protoplasm. *C*, the surface becomes indented by furrows; all the nuclei of the blastoderm-cells are shown in the act of division. *D*, the blastoderm-cells in the form of long cylindrical epitheloid cells. *b*, peripheral protoplasm; *bz*, blastoderm-cells; *d*, food-yolk; *dz*, yolk-cells; *fz*, so-called cleavage-cells; *i*, inner peripheral protoplasm.

According to **Weismann** (No 89) in *Rhodites* and *Biorhiza aptera* (*Cynipidae*) the first cleavage-nucleus divides at first into two nuclei which shift apart in the direction of the longitudinal axis of the egg, and, according to their positions, are known as the anterior and posterior "pole nuclei."* While the anterior nucleus remains inactive for some time, the posterior, by a kind of budding (?), gives rise to numerous nuclei, which take part in the formation of the blastoderm. The anterior nucleus, on the contrary, after the completion of the blastoderm, is said to produce by division the nuclei of the so-called inner germ-cells or yolk-cells.

The process of the formation of the blastoderm in larger eggs rich in yolk was first followed in detail by **Bobretzky** (No. 6) and **Graber** (No. 149), with the help of sections. More recently **Blochmann** (No. 5) has made investigations on the *Muscidae* with which the statements of **Heider** (No. 38) concerning *Hydrophilus* agree. The cleavage-nuclei at first lie at the centre of the egg, more or less in the longitudinal axis (Fig. 131 *A*). Each of these nuclei (*f*) is surrounded by a star-like mass of protoplasm, and the whole is therefore not

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* [This term is used only to describe the position of these two first cleavage-nuclei in the elongate egg, and has no connection with the nuclei of the polar bodies, or with the "pole-cells," p. 352.—Ed.]

unlike a wandering amoeboid cell. Since, however, all these protoplasmic islands are connected by a fine network of processes, the whole egg constitutes a syncytium, the yolk being contained in the meshes. Nevertheless, although these formative centres are not yet distinctly marked off they are already called (though inaccurately) *cleavage-cells*.

In later stages these "cleavage-cells" shift somewhat nearer the surface of the egg, and become arranged to form a sphere (Fig. 130 *A*, 131 *B*) almost parallel to the latter. In sections of the egg they therefore appear arranged as a circle (Fig. 130 *A*). Gradually, during further processes of division, they reach the surface of the egg and fuse with the peripheral protoplasm found there (Figs. 130 *B* and 131 *C*). Division into separate cell-territories corresponding to the cleavage-nuclei now takes place (Figs. 130 *C* and 131 *D*) by the appearance of furrows that press in from the surface, and gradually traverse the whole of the peripheral protoplasm (Fig. 130 *D*). After the surface of the egg has been covered in this way with an epithelium (blastoderm), there follows, in many Insects (*Chironomus*, *Musca*, *Hydrophilus*), the separation of the so-called inner peripheral protoplasm (Fig. 130 *D*, *i*), *i.e.*, of a layer of protoplasm containing coarse granules which develops between the blastoderm and the central yolk-mass. By taking up this layer of protoplasm, the blastoderm-cells increase in height, and now form a cubical or

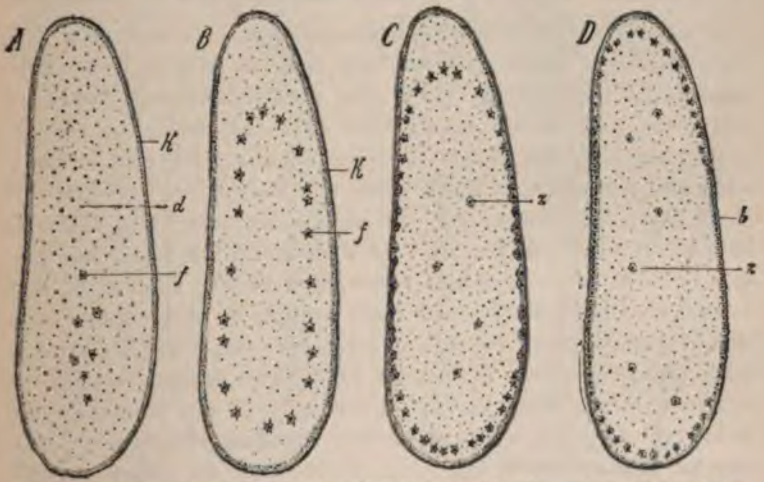

FIG. 131.—The formation of the blastoderm in *Hydrophilus* (after HEIDER). *b*, developed blastoderm; *d*, food-yolk; *f*, so-called cleavage-cells; *k*, peripheral protoplasm; *z*, yolk-cells.

cylindrical epithelium which continuously covers the surface of the egg.

The point at which the cleavage-cells first reach the surface varies in the different groups of Insects. In the *Muscidae*, according to GRABER, the formation of the blastoderm first commences at the posterior pole of the egg, while in *Apis* (KOWALEVSKY), *Pieris* (BOBRETZKY, No. 6), and *Chironomus* (WEISMANN, No. 89), the first blastoderm-cells were noticed at the anterior pole. In *Hydrophilus* (HEIDER, No. 38) the blastoderm first forms round the middle of the egg as a transverse girdle, somewhat nearer the posterior pole of the egg, and develops last at the poles. In *Blatta* (WHEELER) and *Gryllotalpa* (KOROTNEFF) the first cells forming the blastoderm appear on the future ventral surface. As it is at this side that the rudiment of the germ-band arises, the early appearance of the blastoderm-cells at this part recalls the premature development of the blastoderm often occurring in the Crustacea in the region of the embryonic germ-zone (Vol. ii., p. 115). A similar development is found in *Oecanthus* (AYERS, No. 1).

A method of blastoderm-formation differing somewhat from the above and more normal type has been observed in some Orthoptera (*Blatta* and *Gryllotalpa*). As a rule, the "cleavage-cells" increase within the food-yolk so rapidly that when they reach the surface of the egg they are closely crowded together, and here at once constitute a continuous epithelium, but this is not the case in *Gryllotalpa* (WEISMANN, No. 89, and KOROTNEFF, No. 47) and in *Blatta* (WHEELER, No. 95). In these forms the first "cleavage-cells," which are comparatively few in number,* migrate to the ventral surface of the egg and there multiply so that separate cell-islands are temporarily formed. Only in later stages do the cleavage-cells, greatly increased in number by division, become distributed equally over the whole surface of the egg. It was maintained by WHEELER that, in *Blatta*, when the amoeboid cleavage-cells had reached the surface of the yolk, their nuclei no longer showed mitotic division, but here (as well as later in the serosa) multiplied by direct or amitotic division.

The question as to the origin of the so-called yolk-cells or vitellophags is of importance. It has been observed that, as a rule, not all the "cleavage-cells" shift to the surface to take part in the formation of the blastoderm, but that a few remain behind within the yolk (Fig. 130 *D*, *dz*, and 131 *C*, *D*, *z*), where they increase in number, obtain equal distribution throughout the yolk, and become the so-called yolk-cells, whose function is to liquefy the mass of food-yolk and to bring about its assimilation. The origin of the yolk-cells from cleavage-cells which have remained in the yolk has

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* [In *Blatta* they are numerous, sixty to eighty cells being found scattered in the yolk before migration commences.—ED.]

recently been definitely maintained among others by **Kowalevsky**, **Blochmann**, **F. Schmidt**, and **Graber** (No. 28) for *Muscidae*, by **Wheeler** for *Doryphora*, and by **Heider** for *Hydrophilus*. **Patten**, on the contrary, has proved in connection with the egg of a Phryganid (*Neophylax*), and **Wheeler** in connection with that of *Blatta*, that in these forms all the "cleavage-cells" migrate to the surface and take part in the formation of the blastoderm, so that there is a stage at which the surface of the egg is covered by the blastoderm, while the centre of the egg is devoid of nuclei. In these cases the so-called yolk-cells only appear later, single blastoderm-cells wandering again into the interior. As we shall see later, even in the forms first described, a secondary increase of yolk-cells takes place by immigration from the blastoderm (or from the germ-band), these forms, in which all the cleavage-nuclei reach the surface and in which the immigration of the yolk-cells only takes place later,

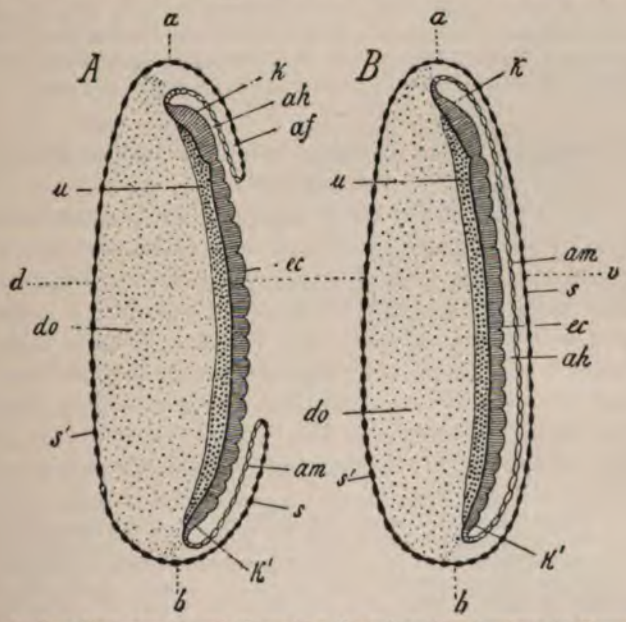

Fig. 132.—Two diagrammatic sagittal sections through an insect-embryo to illustrate the development of the embryonic envelopes. In *A*, the germ-band (*k*, *k'*) is not completely grown over by the amniotic fold. In *B*, the amniotic folds have united and completely cover the germ-band. *a*, anterior, *b*, posterior pole of the egg; *v*, ventral; *d*, dorsal; *af*, amniotic fold; *ah*, amniotic cavity; *am*, amnion; *do*, food-yolk; *ec*, ectoderm; *k*, cephalic end of the germ-band; *k'*, posterior end of the germ-band; *s*, part of the serosa derived from the amniotic fold; *s'*, part of the serosa derived from the undifferentiated blastoderm; *u*, lower layer.

perhaps represent the primitive condition, while in most Insects there is a kind of abbreviation of development which causes some of the cells to remain within the yolk from the first. *Cf.* in this connection the formation of yolk-cells in the Crustacea (Vol. ii., p. 144), Arachnida (pp. 43–45), and Myriopoda (p. 221).

In the case of the *Aphidae* also, WILL (No. 97) has maintained that the yolk-cells arise exclusively through the immigration of cells from the blastoderm during its formation.

As a rule, all the blastoderm-cells are at first of the same shape and size. An exception is afforded by the eggs of the Diptera, in which the so-called pole-cells, to be described later (p. 352), which represent the early differentiation of the genital rudiment, present us with elements which for a moment, indeed, are incorporated in the blastoderm, but are distinguished by their size and their contents from the blastoderm-cells (*cf.* Fig. 174 *C*, *pz*, p. 353, and Fig. 175 *B*, *p*, p. 354).

3. The Formation of the Embryonic Rudiment and the Embryonic Integuments.

A. General view of the Germ-band and the Germ-envelopes.

The embryonic rudiment in the Insecta, as is often the case in the Arthropoda, takes the form of a long band-like thickening, usually extending along the ventral side of the egg, this being known as the *germ-band*, *embryonic band* (Fig. 134 *E*). In most cases the boundaries of the future body-segments are already indicated on this band by consecutive transverse furrows. A cross section through the germ-band of an insect (Fig. 133 *B* and *C*) shows it to be multilaminar. It consists[*] of an outer layer of cells, the *ectoderm* (*ec*),

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[*] We shall here therefore give the name "germ-band" to the whole embryonic rudiment in contradistinction to the transitory portion of the egg, which comprises the food-yolk with its vitellophags and the embryonic envelopes. Such a use of the term "germ-band" is universal in connection with the Arthropoda. It should, however, be pointed out that in the Hirudinea (Vol. i., p. 321) this term is used in another sense, and only embraces a part of the embryonic rudiment. Indeed, the expression "germ-band" is occasionally used as the equivalent of "mesoderm-bands."

[†] According to the published statements, we must assume that cellular embryonic envelopes are not present in the Apterygogenea. They are said to be wanting in the *Poduridae* (ULJANIN, No. 83). A cuticular larval integument, such as is repeatedly found in other groups of Arthropoda (Arachnida and Myriopoda, pp. 9, 58, 97), is said to form in this case. This may be provided with prominences to assist in splitting the egg-integuments, and its presence has been definitely proved by the observations of SOMMER (No. 76) and LEMOINE (No. 51). Indeed, it appears that the Podurid embryo passes through several moults before hatching. From this fact the absence of the amnion might be concluded. GRASSI (No. 33) who observed a dorsal organ in *Japyx* which occurs in the same way in the *Poduridae*, sees in this a proof of the presence of the amnion. Since, however, in the *Poduridae*, this organ develops in the earliest stages of the formation of the germ-band, it seems doubtful whether we may compare it with the dorsal organs developing by the involution of the serosa in the higher Insects (p. 304). We must therefore await further investigations of these points. (See p. 304, and HEYMONS, No. XVI).

and an inner layer which comprises the *entoderm* and the *mesoderm*, and as long as these two germ-layers are not sharply distinguished one from the other, this is known as the inner or lower layer (*u*).

It is characteristic of the Insecta, but only rarely occurs in other Arthropoda (*e.g.*, in the Scorpiones, Fig. 3, p. 5), that the germ-band does not remain freely exposed on the surface of the egg, but is grown over by an amniotic fold rising from its edges (Figs. 132 *A*, *af*, and 133 *B*, *af*), so that the former appears somewhat sunk below the ventral surface. As the amniotic fold extends from all sides over the germ-band, a cavity is enclosed between the two. This is the amniotic cavity (*ah*), which, when the amniotic folds have completely covered the germ-band and have united over it, appears as an entirely closed cavity (Figs. 132 *B* and 133 *C*). (See footnote †, p. 268.)

The germ-band, after its development, thus appears covered by a double cellular envelope derived from the amniotic fold. The outer of these two envelopes is distinguished as the serosa (*s*). This passes without any break of continuity into that undifferentiated portion of the blastoderm which takes no part in the formation of the germ-band (Fig. 132, *s*), and

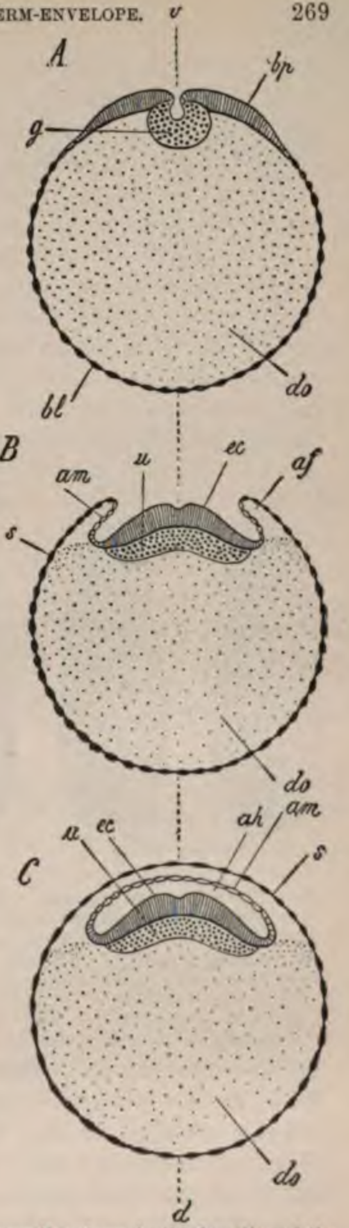

FIG. 133.—Transverse sections through three consecutive stages in the formation of the germ-band and the embryonic envelopes of an insect-embryo. *A*, formation of the ventral plate (*bp*) and the gastrula-invagination (*g*). *B*, rise of the amniotic fold (*af*). *C*, complete overgrowth of the germ-band by the amniotic folds. *v*, ventral, *d*, dorsal surface; *af*, amniotic fold; *ah*, amniotic cavity; *am*, amnion; *bl*, blastoderm; *bp*, ventral plate; *do*, food-yolk; *ec*, ectoderm; *g*, gastrula-invagination; *s*, serosa; *u*, lower layer.

which covers the surface of the food-yolk. This part of the blastoderm, after the completion of the envelopes, is usually reckoned as part of the serosa, so that in this sense we can say that the serosa forms a closed sac covering the whole surface of the egg (Fig. 133 *C*, *s*), one part of it enveloping the surface of the food-yolk and the other that of the germ-band.*

The inner of the two envelopes covering the germ-band which was derived from the inner layer of the amniotic fold is known as the amnion (Figs. 132 and 133, *am*). This, at the edges of the germ-band, is continued into the ectoderm of the latter, the transition being in most cases quite gradual. The amnion and the ectoderm (*ec*) of the germ-band thus together form an epithelial sac closed on all sides, the lumen of which is represented by the amniotic cavity.

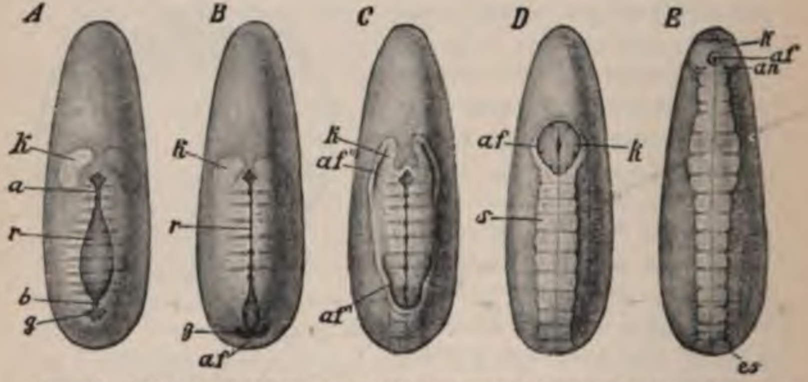

FIG. 134.—Ventral aspect of five stages in the development of *Hydrophilus* (after HEIDER, from LANG'S *Text-book*). The anterior end is directed upwards. *a* and *b*, points at which the blastopore closes; *af*, edge of the amnion-fold; *af'*, caudal fold; *af''*, paired cephalic fold of the amnion; *an*, antenna; *es*, terminal segment; *g*, pit-like invagination (rudiment of the amniotic cavity); *k*, cephalic lobes; *r*, groove-like invagination; *s*, part of the germ-band covered by the amnion.

The origin of the *germ-band* is to be sought in a thickening of the blastoderm on the ventral side of the egg (Fig. 133 *A*, *bp*). While, as was mentioned above (p. 268), the blastodermic cells originally exhibited the same shape and size over the whole surface of the egg, they soon become differentiated in such a way that the cells of the dorsal side flatten to form a thin pavement epithelium,

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* The fact that GRABER (No. 27) observed in *Melolontha* the secretion of a cuticle from the outer surface of the serosa, after the completion of the development of the embryonic envelopes, deserves mention. A certain parallel may perhaps exist between this process and the development of the blastodermic cuticle in the Crustacea and other Arthropoda.

while the cells belonging to the ventral side, owing to their more rapid division, become crowded close together, assume a prismatic form, and thus constitute a columnar epithelium. The ventral thickening of the blastoderm that has thus arisen, and which, in its extent, represents the first rudiment of the germ-band, was named by BALFOUR the *ventral plate* (Fig. 133 *A*, *bp*). The invagination of that part of the ventral plate which lies in the median line (*g*) gives rise to the formation of the lower layer. This invagination, which at a certain stage represents a groove running along the median line for the whole length of the germ-band (Fig. 134 *A* and *B*), must be regarded as the *gastrula-invagination* of the Insecta (for details, see pp. 309 *et seq.*). The lower layer yielded by it (Fig. 133, *B* and *C*, *u*) then extends beneath the whole of the ventral plate up to the edges of the amniotic fold (Figs. 133 *B* and 134 *C*).

It should be mentioned that the ventral plate from its commencement is not in all cases a uniform structure, but sometimes proceeds from several distinct rudiments. Thus it has been pointed out by F. SCHMIDT, in connection with *Musca*, and by HEIDER in connection with *Hydrophilus*, that the anterior and posterior ends of the germ-band appear first, the middle part only developing later. Another originally independent element of the germ-band is afforded in *Hydrophilus* by the rudiments of the cephalic lobes (Fig. 134 *A*, *k*), the independent origin of which was also observed by WILL (No. 97) in the *Aphidae*. These originally distinct formative centres only secondarily unite to form the common rudiment of the germ-band.

The lateral delimitation of the germ-band seems determined by the rise of the amniotic fold, and since, when the amnion is complete, it consists of somewhat columnar cells and, even at later stages, owing to its histological character, more nearly resembles the ectoderm of the germ-band than the serosa, some investigators have assumed a closer connection between the amnion and the germ-band. WILL regards the amnion directly as a part of the germ-band, and GRABER (No. 30) also derives the amnion from the thickened epithelium of the ventral plate.

We have used the term "germ-band" in the usual manner, understanding by it the segmented and already multilaminar embryonic rudiment (consisting of the ectoderm and the lower layer). It is, however, certain that this term may also be applied in a wider sense, as GRABER (No. 30) has recently insisted, to the embryonic rudiment of earlier stages, in which segmentation and the formation of the germ-layers has not yet commenced, presupposing that the embryonic rudiment as such is distinctly marked off from the rest of the egg.

From the time of its origin onwards, the germ-band grows continually in length (Fig. 134 *A* to *E*), and in many cases extends in such a way that it no longer covers only the ventral side of the egg, but its anterior and posterior ends bend round to the dorsal side of the egg. This extension of the germ-band to the dorsal side may, in some cases (*Phryganeidae*, *Chironomus*), go so far that the anterior and posterior ends almost come into contact (Fig. 141, p. 283). The germ-band thus appears at these early stages, *i.e.*, roughly speaking, during the first half of its embryonic development, dorsally flexed. In the later stages, in consequence of the development of organs, and the more complicated shape thus brought about, the band shortens by contraction, so that finally the oral aperture comes to lie at the anterior pole of the egg, and the anal aperture near the posterior pole (Fig. 143, *m* and *an*). These positions of the apertures are very typical of Insect embryos at later stages. The embryonic rudiment now no longer appears curved dorsally, but is straight. Indeed, curvature in an opposite direction often takes place, the most posterior segment of the embryo appearing ventrally curved (*Phryganeidae*, Lepidoptera, *Hydrophilus*, *Blatta*, etc., Fig. 142 *C*, p. 285, and Fig. 143 *B*, p. 286).

GRABER (No. 30) has recently pointed out that the Insects may be divided into two groups, according to the extension and the increase in the length of the germ-band. In the first group the conditions of growth of the embryo described above prevail, while, in the other forms (*e.g.*, *Blatta*, *Stenobothrus*) the embryonic rudiment from the very first extends over only a quite short area of the periphery of the egg, and during the whole of the later development never grows in the same way as forms belonging to the first group. In forms in which the germ-band is short, the dorsal curvature is naturally not noticeable in the earlier stages, and the germ-band appears to be straight. The growth of the embryonic rudiment in length also progresses more equally during the whole development. Shortening is not perceptible in the later stages. Insects might therefore be divided into two groups as having, on the one hand, germ-bands which are long at first and shorten later, and, on the other hand, germ-bands which remain from the first comparatively short. This distinction, however, does not appear to us to be based upon differences of any importance.

B. The distinction between the superficial and the immersed Germ-band.

The general description of the position and the origin of the germ-band and the embryonic envelopes, given above (p. 268, etc.), only holds good for some of the Insecta. These conditions are to be found in many Orthoptera (*Blatta*), the *Phryganeidae*, Lepidoptera, Hymenoptera, many Diptera (*Chironomus*), and to some extent in the Coleoptera. In details, however, an abundance of variations which will be mentioned later are found to occur; these may be traced back to the shape of the egg, the amount and distribution of the food-yolk, and also to some extent to the vestigial condition of the embryonic envelopes. In other groups of Insects (Pseudoneuroptera, Hemiptera), on the contrary, we find that the phenomena manifested in the formation of the germ-band and the embryonic envelopes, as well as the position of the former, differ still further from those which we described above, and which we took as a starting-point for the sake of clearness. We must now deal with all these conditions in detail.

From the above description of the rise of the amniotic fold (Figs. 132 and 133, *af*), it becomes evident that a cavity, continuous with the space containing the food-yolk, extends in between the serosa and the true amnion. It is thus possible for spherules of food-yolk to pass into this cavity and entirely to fill it (Fig. 135). In this case the amnion and the serosa are separated from each other by a somewhat wide space filled with food-yolk, whereas, in other cases, where the food-yolk does not penetrate this cavity, the amnion and the serosa are in direct contact (Fig. 158 *B–F*). We may thus divide the eggs of Insects into two groups, according to the presence or absence of this space between these two embryonic envelopes.

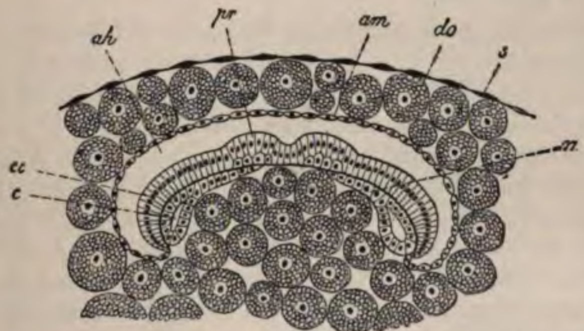

FIG. 135.—Section through the germ-band of a Lepidopterous Insect (combined from drawings by BOBRETZKY and HATSCHEK). *ah*, amniotic cavity; *am*, amnion; *c*, coelomic cavity; *do*, food-yolk (divided up into separate masses, each containing a nucleus); *ec*, ectoderm; *m*, mesoderm; *pr*, thickenings of the ectoderm, representing the rudiments of the ventral nerve-cords; *s*, serosa.

1. Eggs in which the germ-band is *superficial*, *i.e.*, in which the elements of the food-yolk have not penetrated into the space between the amnion and the serosa. The germ-band is here comparatively superficial (Figs. 132, p. 267; 133, p. 269; 140 *A*, p. 281; 143, p. 286).

2. Eggs in which the germ-band is *sunk* or *immersed*, the space between the amnion and serosa being filled by particles of food-yolk. In such cases the germ-band appears, as compared with type 1, more deeply sunk within the egg (Figs. 135, 136 *C–E*, and 142, p. 285).

The germ-band is superficial in many Orthoptera (*Oecanthus*, *Gryllotalpa*, *Blatta*, *Mantis*), in many Hemiptera (*Corixa*), in the *Phryganeidae*, the Diptera, and the Hymenoptera. In the Coleoptera also, the greater part of the germ-band appears superficial, but its posterior end is in the first stages immersed. An immersed germ-band occurs in the *Libellulidae*, many Hemiptera (*Pyrrhocoris*), many Orthoptera (*Stenobothrus*), and in the Lepidoptera.

C. The distinction between the invaginated Germ-band and the Germ-band that has been overgrown by the Membranes.*

With regard to the manner in which the germ-band arises and to its position, there are two opposite types among the Insecta, these, however, being connected by means of transitional forms. In the one type the ventral plate is invaginated into the inner part of the egg, and in the other the amniotic folds rising from its edges grow over it.

1. When the germ-band during its formation is *invaginated*, e.g., *Libellulidae*, Brandt (No. 7), its first rudiment appears in the form of a small thickening of the blastoderm lying ventrally in the posterior half of the egg (ventral plate, Figs. 136 *A*, *bp* and 137 *A*), in the posterior region of which invagination soon takes place (Fig. 136 *A*, *kh*). The lumen of this invagination is the first rudiment of the amniotic cavity (Fig. 136 *B*, *ah*); the thickened ventral portion of its wall (*k*) forms the germ-band, while the thinner dorsal portion gives rise to the amnion (Fig. 136 *B*, *C*, *am*). The blind end of the invagination denotes the later anal end of the germ-band (*k'*). Since, however, the invagination grows from behind forward in the egg, it results that the primitive position of the germ-band appears to be the exact reverse of its later position, its posterior end becoming forwardly directed, while its cephalic end lies near the posterior pole of the egg. In a similar way, that surface of the germ-band which was primarily on the ventral surface of the egg becomes secondarily turned towards the dorsal side of the egg, so that the ventral surface of the developing embryo is now seen through the dorsal wall of the egg. To bring the germ-band into its definitive position the process described as reversal, rotation, eversion, or revolution, which will be described below, is needed.

It should be mentioned that in eggs of this type the anterior end of the germ-band, which is distinguished by the extension of the cephalic lobes (Fig. 136

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* On this distinction rests the division of Insects into those with inner and those with outer germ-bands (inner and outer germs, or entoblastic and ectoblastic forms, Graber). Graber has recently suggested the terms entoptic and ectoptic germ-formation to describe these categories. We have not adopted these terms, because they are liable to confusion with the superficial and immersed germ-bands, given above (p. 273).

C, *D*, *k*), does not take part in the process of invagination. It remains on the true ventral surface of the egg, and only becomes covered by the growth of the embryonic envelopes (*af*) taking place in the usual manner. Thus the relation of the anterior portion of the germ-band in this type answers to the description given below for the second type.

2. When the formation of the germ-band is accompanied by the *growing over of an amniotic fold*, the ventral plate, and the germ-band which develops out of it retain throughout the course of development the position which is typical of the later stages in all Insect eggs. This type of development which is exemplified in the Diptera (*Chironomus*, *Simulia*, *Cecidomyia*) is the one already described (p. 268, etc.). The germ-band in this case essentially belongs to the ventral side of the egg. Its anterior end corresponds to the anterior pole of the egg, and its posterior end to the posterior pole (if we do not take into account the dorsal extension mentioned above, p. 271). There is therefore no reversal or rotation in this case. The embryonic envelopes are formed by simple folds which

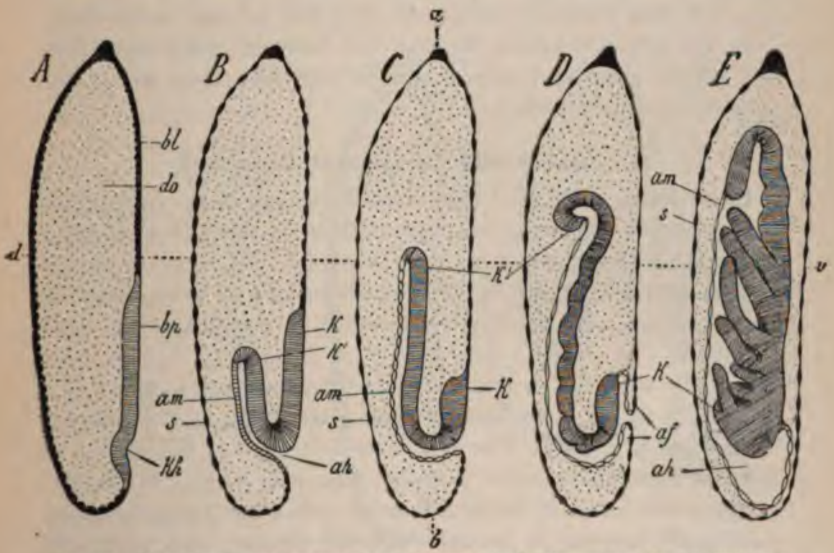

FIG. 136.—Diagrammatic median sections, to illustrate the development of the Libellulid egg (after BRANDT). *A*–*C*, development of the germ-band (*K*, *K'*) accompanied by invagination. *D*, development of the amniotic folds (*af*) which grow over the cephalic end of the germ-band. *E*, the aperture of the amniotic cavity is closed. *v*, ventral side of the egg; *d*, dorsal side; *a*, anterior, *b*, posterior pole of the egg; *af*, amniotic fold; *ah*, amniotic cavity; *a*, amnion; *bl*, blastoderm; *bp*, ventral plate; *do*, food-yolk; *k*, cephalic end of the germ-band; *k'*, anal end of the germ-band; *kh*, germ-prominence or commencing invagination; *s*, serosa.

rise from the edges of the germ-band (Figs. 132 and 133, pp. 267 and 269).

If we take into consideration the position of the germ-band at the time of its formation, the two types here distinguished might also be defined as a type with the germ-band inversely placed, and one with the germ-band normally placed. It would be still simpler to define them as types either with or without the reversal or rotation. It might indeed be objected that, in the germ-band that is overgrown, changes of position have also occasionally been observed, and these are often very difficult to distinguish from true reversal or rotation.

In the order Coleoptera, we shall find forms in which the formation of the germ-band affords a direct transition from one of the types above distinguished to the other.

D. Insects with Invaginated Germ-band.

Libellulidae. We shall first consider the egg of the *Libellulidae* (A. Brandt, No. 7) as the best representative of this type of development. This family, as we shall see below (p. 288), seems to exhibit conditions which might be direct modifications of those found in the Myriopoda, and which must therefore be regarded as the more primitive.

In *Calopteryx*, the first rudiment of the germ-band is found in a thickening of the blastoderm (ventral plate) lying in the posterior ventral half of the egg. The most posterior portion of the germ-band soon becomes pressed into the egg (Fig. 137 *A*, *g*). While this invagination, which by many authors is called the *germ-prominence*, continually deepens, it becomes directed forward and grows out towards the anterior pole of the egg (Fig. 137 *B* and *C*). The lumen of the invagination is the first rudiment of the amniotic cavity. A difference in the thickness of the two walls of the invagination is very soon perceptible. The dorsal wall which represents the amnion (*am*) becomes gradually thinner and its cells flatten, while the other wall thickens and represents the actual germ-band (*ps*). Almost the whole of the germ-band is here invaginated into the egg, its posterior end pointing forward. Only a small part of the band, its primitive anterior end, retains for a time the superficial ventral position of the original thickening of the blastoderm (Fig. 137 *C*); this soon broadens out to form the cephalic lobes. This part now becomes completely grown over by a circular amniotic fold derived from the surrounding blastoderm. When this circular fold closes over the cephalic lobes, the amniotic cavity is cut off from the exterior (Fig. 138 *A*). The thin layer of the blastoderm surrounding the egg, which has retained its superficial position, now represents the serosa.

In the subsequent stage, which is characterised by the possession of limb-rudiments, the remarkable position of the germ-band can be distinctly recognised (Fig. 138 *A*). We see that its cephalic end (*v*) is directed towards the posterior pole of the egg, while its hook-like posterior end (*ab*) is directed towards the anterior pole. We can also see, from comparison with other stages (Fig. 138 *C*), that the ventral side of the germ-band on which the limb-rudiments form is turned to the dorsal side of the egg. The definitive position of the embryo is brought about by a process of reversal or rotation of the germ-band, the embryo undergoing rotation round its transverse axis, and being at the same time evaginated from the amniotic cavity (Fig. 138 *B*). This process is commenced by the fusion and subsequent rupture of the amnion and serosa near the cephalic region. This rent gives rise to an opening into the amniotic cavity at the very point where the original aperture of the invagination was situated, and through this aperture first the head and then the consecutive segments of the germ-band emerge and become applied to the ventral portion of the egg-shell, the head shifting towards the anterior pole (Fig. 138 *C*). In proportion as the embryo emerges from the amniotic cavity, the latter diminishes in size, and finally completely disappears, the embryo being now only surrounded by the egg-shell.

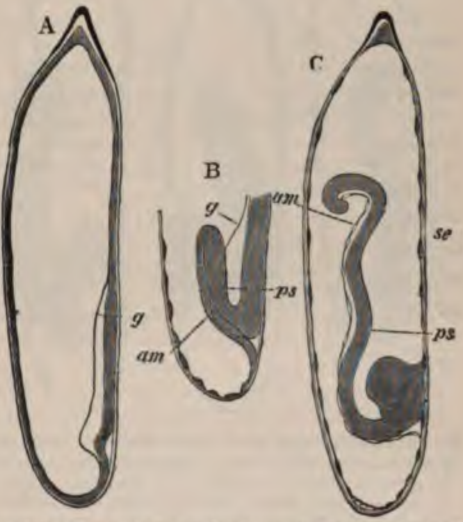

Fig. 137.—Three stages of development of the embryo of *Calopteryx* (after Brandt, from Balfour's *Text-book*). The embryo is represented inside the egg-shell. *am*, amnion; *g*, lateral edge of the ventral plate; *ps*, rudiment of the germ-band; *se*, serosa.

As the germ-band now lies on the surface of the egg, the area occupied by the serosa has become considerably diminished (Fig. 138 *C*). This envelope now contracts towards the anterior pole of the egg, thickening considerably at the same time (Fig. 138 *C*, *se*). In consequence of this contraction, the edge of the rent where the serosa and the amnion coalesced and finally the amnion itself are drawn anteriorly over the food-yolk (Fig. 138 *C*, *se* and *am*), so that the two envelopes together finally form a sac lying dorsally to the embryo; this sac is filled with food-yolk, and may be defined as a kind of (dorsal) yolk-sac. As the lateral and dorsal parts of the embryo now develop further, the contents of the yolk-sac are taken up more and more into the intestinal cavity, which communicates with the sac, and are used up, so that finally, by a process to be described later, the serosa itself is (apparently) drawn into the embryo and assimilated (p. 304).

FIG. 138.—Three stages in the development of *Calopteryx* (after BRANDT, from BALFOUR'S *Text-book*). The embryo is represented inside the egg-shell. *a*, secondary opening of the amniotic cavity, through which the embryo emerges; *ab*, abdomen; *am*, amnion; *at*, antenna; *md*, mandible; *mx*¹, *mx*², first and second maxillae; *oe*, oesophagus; *p*¹, *p*², *p*³, the three pairs of thoracic legs; *se*, serosa; *v*, anterior end of the germ-band.

Since the germ-band of the *Libellulidae* arises by an invagination which grows into the interior of the egg, it is seen that the amnion and serosa are here separated by a wide space filled with food-yolk. The germ-band of the *Libellulidae* is therefore immersed. Its cephalic end, however, is excepted from this immersion, and so belongs to the superficial type.

Rhynchota. The type of development of the germ-band described above for the *Libellulidae* occurs also, as far as is at present known, in all Rhynchota. METSCHNIKOFF (No. 55) and BRANDT (No. 7) thus found in *Hydrometra*, and GRABER (No. 27) in *Pyrrhocoris*, conditions of development of the egg which in all important points agreed with those observed in the *Libellulidae*.

A modification of the type described is met with in *Corixa* (METSCHNIKOFF, No. 55; BRANDT, No. 7). In this form the germ-prominence, which becomes invaginated at the posterior pole, is indeed also at first surrounded by food-yolk, but very soon becomes closely applied to the dorsal side of the egg, so that the serosa and the amnion are here in close contact. The germ is consequently not immersed, but superficial. In other respects, the process of rotation and the acquisition of its definitive position by the embryo occur in exactly the same way as in the *Libellulidae*.

The germ-bands of the Pediculina and the Mallophaga also, according to MELNIKOFF (No. 53), agree with regard to position with that of the *Libellulidae*. But the condition in these cases is to some extent simpler, as the aperture of invagination into the amniotic cavity remains permanently open. An invaginated germ-band is also found in the *Physapoda* (DOHRN, No. 21; JORDAN, No. 44).

The processes of development found in the eggs of the Phytophthires form a direct sequence to those described for the *Libellulidae*. The descriptions given by METSCHNIKOFF (No. 55) and BRANDT (No. 7) of the development of the viviparous *Coccidae* (*Aspidiotus*, *Lecanium*) show almost complete agreement with the *Libellulidae*; and the *Psyllidae* also, according to METSCHNIKOFF, seem to follow the same course. Certain peculiarities, on the other hand, are shown by the summer eggs of the viviparous *Aphidae*, which pass through their development within the egg-follicle. The eggs of these forms that develop parthenogenetically do not, as WILL (No. 97) has pointed out, undergo the full process of maturation found in other insect eggs. The former exhibit a precocious embryonic development, which commences at the stage when only the very first phenomena of maturation are to be found in the appearance of small drops of deutoplasm. After the development of the blastoderm, the egg contains only a small amount of food-yolk, which soon disappears (*primary food-yolk*, Fig. 139 *A*, *do*), and in which single yolk-cells are found. In the stages that follow, however, the embryo is provided with a fresh mass of yolk (secondary yolk, *pseudovitellus*, *sd*) through the development of a kind of placental formation from the follicular epithelium of the parent (Fig. 139 *A*, *sd*). At the posterior pole of the embryo, at which the formation of the blastoderm is not fully completed, and where consequently there is a gap in the blastoderm,* a fusion occurs with the corresponding part (x) of the follicular epithelium (*f*). A mass of cells here develops by repeated division as an outgrowth of the follicular epithelium. This mass, by the degeneration and complete disintegration of the cells composing it, becomes transformed into an accumulation of yolk-spherules (*secondary yolk*), and the yolk-material thus produced is projected into the interior of the embryo through the gap in the blastoderm (Fig. 139 *A*, *sd*). The secondary yolk-mass, which thus comes to lie in the primary body-cavity, and into which yolk-cells (*dz*) soon wander from the embryo, remains for some time connected by means of a strand of yolk with that part of the follicular epithelium from which it originated.

The development of the germ-band takes place in the *Aphidae* by an invagination at the posterior pole in exactly the same way as in the *Libellulidae*. This invagination develops round the gap in the blastoderm already mentioned (Fig. 139 *A*). It is consequently not closed at its inner end, this being the aperture through which the secondary yolk enters into the interior

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* This gap has been called the blastopore by WILL, and the immigration of yolk-cells proceeding from this point has been assumed to be gastrulation, a view which we cannot share.

of the egg. Only after the secondary yolk has withdrawn into the primary body-cavity, and the connective strand has been absorbed, does this aperture or gap close (Fig. 139 *B*), and the invagination then assumes a shape exactly recalling the corresponding stage in the *Libellulidae*. As the rudiment of the germ-band continues to grow, it develops a hook-like curvature (Fig. 139 *C*), which may later become double (Witlaczil, No. 98). Certain changes in position also take place. The curved rudiment, which is at first symmetrical with regard to the median plane, is soon too long to retain its position, and certain deviations in a lateral direction occur. The outer aperture of the

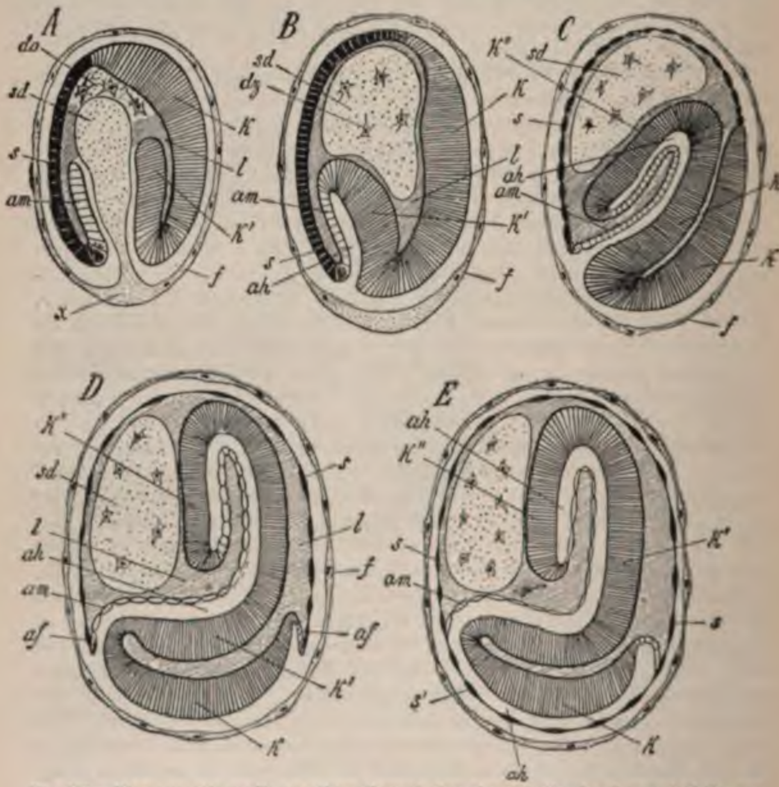

Fig. 139.—Diagrammatic median sections through five stages in the development of the egg of a viviparous *Aphis* (adapted from Will). The orientation agrees with that in Fig. 136. The genital rudiment is omitted. *A*, invagination of the germ-band (*k'*) and growing in of the secondary yolk (*sd*). *B*, closing of the pore through which the secondary yolk was taken in. *C*, hook-like flexure of the posterior end of the germ-band (*k''*). *D*, rise of the amnion-folds (*af*). *E*, development of the cephalic serosa (*s'*). *af*, amniotic folds; *ah*, amniotic cavity; *am*, amnion; *do*, remains of the primary food-yolk with its yolk-cells; *dz*, yolk-cells; *f*, follicle-epithelium; *k*, cephalic end of the germ-band (cephalic lobes); *k'*, posterior section of the germ-band; *k''*, posterior end of the germ-band bent in like a hook; *l*, primary body-cavity; *s*, serosa; *s'*, cephalic serosa; *sd*, secondary yolk; *x*, point at which the secondary yolk forms.

amniotic cavity, which originally belonged to the posterior pole, in the course of further development shifts more to the dorsal side. At the same time, the rudiments of the cephalic lobes (*k*), which have arisen as blastodermic thickenings and which formerly lay at the anterior pole of the egg, shift backward over the ventral side so that finally they extend over the posterior pole (Fig. 139 *D*). The whole of this blastodermic thickening is not, as in the *Libellulidae*, included in the invagination of the germ-band, and its true anterior end is therefore not at first covered by the embryonic envelopes. Soon, however, a circular amniotic fold appears surrounding the primitive anterior end of the germ-band and the aperture of invagination (Fig. 139 *D*, *af*). This circular fold at the time of its rise consists, like every other amnion-fold, of two layers (amnion and serosa). In the course of further growth, however, the serosa outstrips the amnion, so that the cephalic lobes appear covered by only one epithelial cell-layer, the so-called *cephalic serosa* (Fig. 139 *E*, *s'*).*

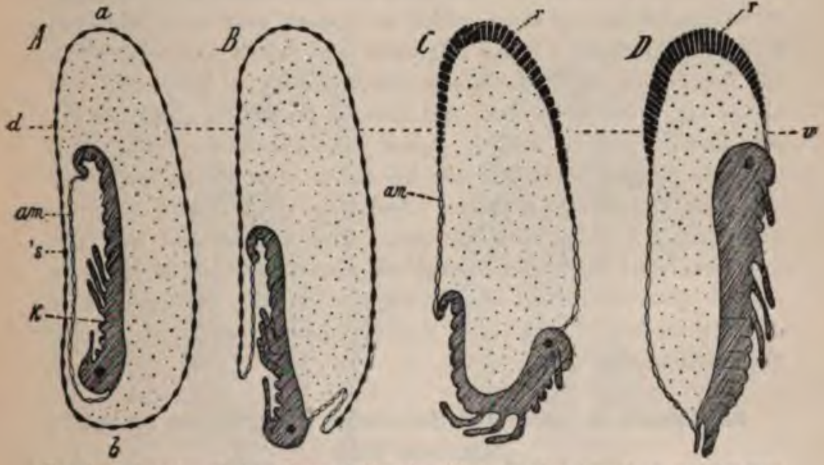

FIG. 140.—Rotation of the embryo of *Oecanthus* (diagrams after AYERS). *a*, anterior pole of the egg; *am*, amnion; *b*, posterior pole of the egg; *d*, dorsal side of the egg; *k*, germ-band; *r*, dorsal plate (caused by the contraction of the serosa); *s*, serosa; *v*, ventral side of the egg.

The other, later processes of development—the rupture of the cephalic embryonic envelope, the evagination of the embryo through the aperture thus produced, and the rotation of the germ-band occur in just the same way as in the *Libellulidae*.

The ontogeny of the *Aphidae* has been described chiefly by BRANDT (No. 7), METSCHNIKOFF (No. 55), WITLACZIL (No. 98), and WILL (No. 97). In the above account we have principally followed WILL.

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* This is a case of the imperfect development of the amnion, such as has been asserted for certain Hymenoptera. It should be mentioned that the account given by BRANDT makes it appear possible that the embryonic envelopes in the cephalic region in the *Coccidae* (and perhaps even also in the *Libellulidae*) develop in the way described by WILL in connection with the *Aphidae*. In this case, in these forms also, the envelope covering the cephalic region would consist of a single layer of cells.

In this type of development we must also include one of the *Gryllidae*, *Oecanthus*, although by so doing we place this form in opposition to the other Orthoptera. In this genus the first rudiment of the germ-band, indeed, does not arise by invagination as has been shown by AYERS (No. 1), but forms as a short ventral plate which is overgrown by the amniotic fold. The inner layer of the fold (the amnion), as in the cephalic fold of the *Aphidae*, does not at first grow over it as rapidly as the outer layer. The serosa therefore at first forms the only complete covering of the germ-band. The amnion, however, grows out later under the serosa and becomes closed, so that the embryo is finally covered by a double cellular envelope. The germ-band is therefore in this case to be classed among those which are grown over by a fold, and it is also superficial. It lies originally (and this is the point which has determined us in the above classification) on the dorsal side of the egg, with its cephalic end directed posteriorly (Fig. 140 *A*), and thus in position entirely agrees with *Corixa* (p. 279). It is therefore obliged, when the rent has taken place in the embryonic envelopes, to undergo a process of rotation (Fig. 140 *B*, *C*, *D*) so as to attain its definitive position. This process and the later degeneration of the serosa through the formation of an invagination (dorsal tube) show such complete agreement with the processes in other examples of this type that we feel justified in classing *Oecanthus* among them.

E. Insects in which the Germ-band is overgrown by the Amniotic Fold.

Orthoptera genuina. In all the forms belonging to this group as yet investigated, with the exception of *Oecanthus*, the germ-band lies from the first on the ventral side of the egg, with its cephalic end pointing anteriorly. In these therefore there is no rotation of the germ-band. The embryonic envelopes arise through the formation of folds. The germ-band is in most cases comparatively short (*Blatta*, CHOLODKOWSKY, No. 19, and WHEELER, No. 95; *Stenobothrus* and *Mantis*, GRABER, Nos. 26 and 30). Only in *Gryllotalpa* (KOROTNEFF, No. 47) does the germ-band attain a considerable length, and consequently appears with its anterior and posterior ends bent over towards the dorsal side. In all these forms the posterior (abdominal) end of the germ-band in later stages appears flexed ventrally, as is also the case in the *Libellulidae*, Rhynchota, *Oecanthus*, *Phryganeidae*, in many Coleoptera, and to a still greater degree in the Lepidoptera and certain Hymenoptera. This curvature becomes lost and the abdomen straightens as a rule even before hatching.

It should be mentioned that in *Stenobothrus* the amniotic fold forms at a very early period in the development of the germ-band. At a time when gastrulation is commencing and the ventral plate is still round and shield-like, the latter is already grown over by the amniotic fold (GRABER, No. 26). In *Gryllotalpa*, the embryonic envelopes develop in the form of two folds rising laterally. In *Blatta*, a caudal fold and paired cephalic folds corresponding to the two cephalic lobes appear first (as in the Coleoptera). The germ-band in the Orthoptera is, as a rule, superficial. Only in *Stenobothrus* does it become immersed by the appearance of particles of food-yolk between the two enveloping layers, a condition which we shall meet with again in the Lepidoptera.

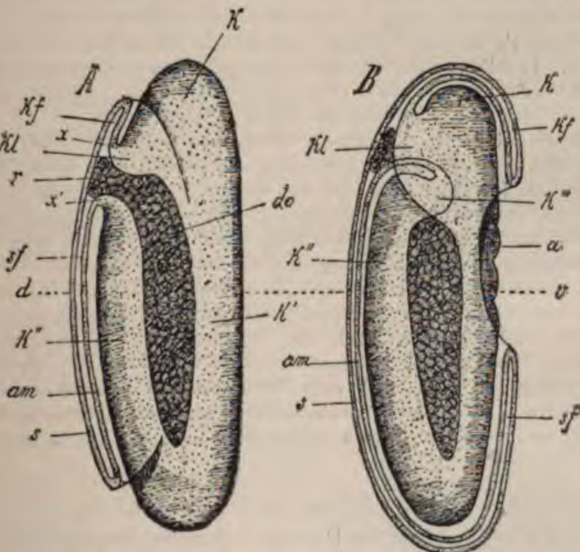

FIG. 141.—Lateral aspect of the egg of *Chironomus* in the stage at which the embryonic envelopes develop (diagram adapted from WEISMANN and KUPFFER). *A*, showing the commencement of the cephalic and caudal folds (*kf* and *sf*). *B*, union of the two folds laterally and their continuous advance over the germ-band. *v*, ventral side; *d*, dorsal side; *a*, uncovered portion of the germ-band; *am*, amnion; *do*, food-yolk; *k*, cephalic end of the germ-band; *k'*, ventral portion of the germ-band; *k''*, portion of the germ-band bent over dorsally; *k'''*, hook-like bend of the posterior end; *kf*, cephalic fold of the amnion; *kl*, cephalic lobe; *r*, dorsal umbilical passage; *s*, serosa; *sf*, caudal fold of the amnion *x*, *x'*, union of amnion with the ectoderm.

Diptera. In all Diptera as yet examined, the germ-band attains a considerable length; it thus not only covers the ventral side, but its two ends bend over dorsally, the posterior end extending very far forward (Fig. 141), so that on the dorsal side of the egg they are seen lying somewhat near each other (x, x'). The later development, in which the posterior end of the germ-band draws back to the posterior pole of the egg, is therefore attended by great shortening of the embryonic rudiment.

The amniotic fold does not here arise simultaneously along the whole edge of the germ-band, but a fold first rises round the cephalic end (*kf*) and a second at the posterior end (*sf*) of the germ-band (*cephalic* and *caudal folds* of the amnion). Only later do folds form at the sides of the germ-band and connect the cephalic with the caudal fold (*Chironomus*, WEISMANN, No. 87, and KUPFFER; *Simulia*, METSCHNIKOFF, No. 55).

As the ends of the germ-band are bent over dorsally and lie very near each other, the edges of the amnion also, which arise from the ectoderm in front of and behind the ends of the germ-band (at x and x' in Fig. 141 *A*), lie near each other. It follows that the region in which the serosa lies directly on the surface of the food-yolk (r) is in these forms very limited. Similar conditions will be met with in the Lepidoptera and the *Phryganeidae*.

The germ-band in the Diptera is throughout superficial; only its most posterior end, in *Chironomus* and *Simulia*, and possibly also in the *Muscidae*, appears bent in the shape of a hook and sunk into the yolk (Fig. 141 *B*, k'''). We have here an approach to conditions to be described in the Coleoptera.

The fact that in a few Diptera the amniotic folds remain imperfect and never completely grow over the germ-band deserves mention. This is the case, according to METSCHNIKOFF (No. 55), in the embryos of the viviparous *Cecidomyia* larvae, in which the cephalic and caudal folds appear as rudiments, but do not develop further. It is also the case, according to KOWALEVSKY and GRABER (Nos. 27 and 28) in the *Muscidae*, in which the cephalic fold remains extremely small, and only the caudal fold develops somewhat more distinctly. In the later development of the embryo, these folds simply flatten out again and then take a certain part, as it appears, in the development of the dorsal integument.

Trichoptera. The conditions to be observed in the rounded egg of the *Phryganeidae*, as PATTEN found in *Neophylax* (No. 65), approximate very closely to the normal type of the Diptera (*Chironomus*). The very long, superficial germ-band here also covers the greater part of the periphery of the egg, so that its anterior and posterior ends almost touch dorsally. We shall see that even the phenomena of degeneration of the germ-envelopes in the two groups belong essentially to the same type (GRABER, No. 27).

Lepidoptera. The Lepidoptera also, in the general conditions of the germ-band and the embryonic envelopes, stand very near the two last groups. A remarkable point in their development is that the amniotic fold forms at a very early stage of the development of the germ-band (as in *Stenobothrus*, p. 282), at a time when the rudiment of the band or ventral plate is only a round, shield-like thickening of the blastoderm (Fig. 142 *A*), from the edge of which the amniotic fold rises. Only later does the germ-band begin to lengthen, and very soon, by the passage of food-yolk masses between the amnion and the serosa, becomes immersed (Fig. 142 *B*). Since, as in the Diptera, increasing length leads to the sharp dorsal curvature of the germ-band, and since the amniotic cavity follows this curvature, that dorsal portion which represents the connection between the embryo and the germ-bands appears to become more and more limited (Fig. 142 *C*, at *x*). There thus develops a dorsal umbilical passage which is here of significance in so far as it represents the passage through which the food-yolk mass taken into the interior of the embryo communicates with that lying between the amnion and the serosa. Taking into account this feature, it might be said that, in the Lepidoptera, the embryo is surrounded by a yolk-sac connected with it through the dorsal umbilical passage.

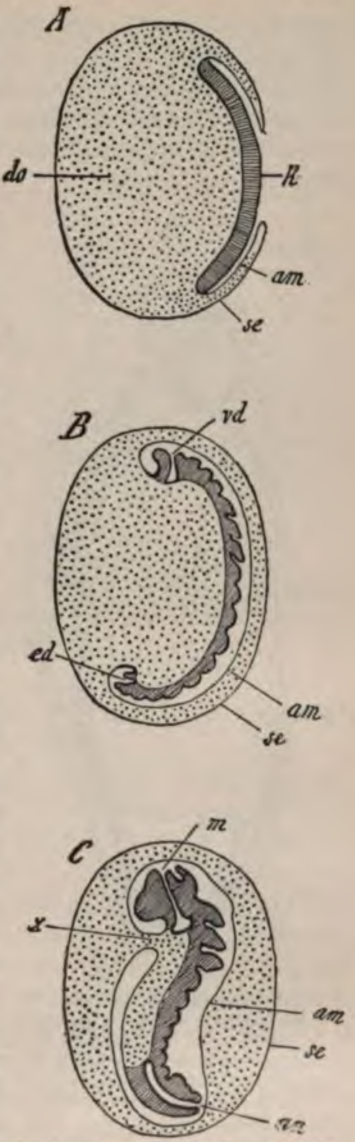

Fig. 142.—Diagram of the formation of the embryonic envelopes in the Lepidoptera (*A* after Kowalevsky, *B* and *C* after Tichomiroff). *k*, germ-band; *am*, amnion; *se*, serosa; *do*, food-yolk; *vd*, invagination of the stomodaeum; *ed*, invagination of the proctodaeum; *m*, mouth; *an*, anal aperture; *x*, dorsal umbilical passage.

Hymenoptera. In the Hymenoptera, conditions are found which agree in essentials with those described for the Diptera. The germ-band here also is always superficial, and is covered by a double cellular envelope (amnion and serosa) formed by the growth ventralwards of a cephalic and a caudal amniotic fold (Fig. 143 *A*). This process has been described by Kowalevsky for *Apis*, and still more clearly by Graber for *Polistes gallica* and *Formica*, and more recently for *Hylotoma berberidis* (Nos. 27 and 30). In *Apis*, at least, the cephalic fold seems to take a greater share in the overgrowth of the germ-band than the caudal fold.

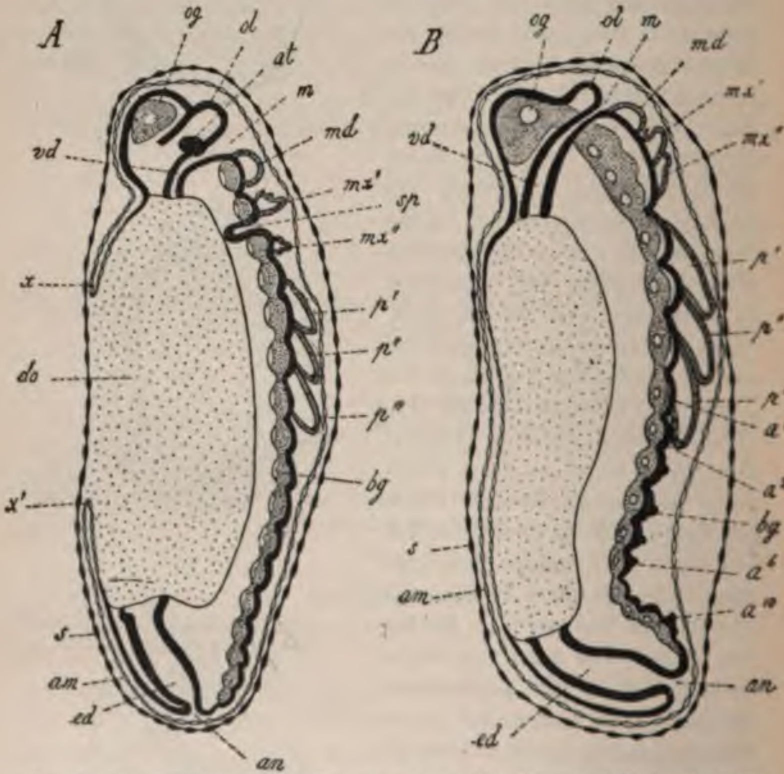

Fig. 143.—Diagrammatic median sections of two stages of development of *Hylotoma berberidis* (after Graber). a^1–a^{10}, first ten abdominal segments; *am*, amnion; *an*, anus; *at*, antenna; *bg*, ventral chain of ganglia; *do*, food-yolk; *ed*, proctodaeum; *m*, mouth; *md*, mandible; mx^1, first maxilla; mx^2, second maxilla; *og*, supra-oesophageal ganglion; *ol*, labrum; p^1, p^2, p^3, the three thoracic limbs; *s*, serosa; *sp*, salivary glands; *vd*, stomodaeum. *x*, x^1, point at which the amnion passes into the ectoderm.

The germ-band in the Hymenoptera remains as a rule comparatively short. It is not longer than the egg (Fig. 143 *A*), and thus remains restricted to the ventral side. On the other hand, the amniotic cavity itself continues to extend over the anterior and posterior ends of the germ-band towards the dorsal surface, thus causing the points where the amnion unites with the ectoderm of the germ-band (*x* and *x'*) gradually to approach one another, a rare condition among the Insecta, but one which apparently also occurs in the Lepidoptera. The dorsal umbilical passage is in this way more and more circumscribed, until, by the fusing of these inner folds and the absorption or rupture of this solid cord, it is completely obliterated (Fig. 143 *B*). The embryo, whose dorsal wall is now completely formed, lies henceforth entirely free within two cellular sacs, the outer one corresponding to the serosa and the inner to the amnion (*s*, *am* in Fig. 143 *B*).

Although the presence of a double cellular envelope (amnion and serosa) in the Hymenoptera can hardly, according to GRABER's recent observations, be doubted, we must here mention that other authors expressly point out that only a single embryonic envelope is present, which then must be assumed to be the serosa. Although some confusion on this point may arise from the fact that the inner envelope (amnion) becomes closely applied to the germ-band (GRABER) and is indistinguishable from the latter, we cannot deny the possibility that the true amnion at first remains stationary, as was described above (p. 281), in the case of the cephalic fold of the *Aphidae* and *Oecanthus* (p. 282). There would then be a separation of the amnion from the serosa at the edge of the amniotic fold, and the latter would grow out independently by a process of overgrowth (*cf.* the description given of the formation of the amnion in the Scorpions, p. 5, Fig. 3). The same conditions were found in *Apis* by BÜTSCHLI (No. 11) and GRASSI (No. 32), also in *Polistes gallica* and *Chalicodoma muraria* by CARRIÈRE (No. 13).*

We are still altogether in doubt as to the presence and constitution of the embryonic envelopes in the Pteromalina (*cf.* on this point the account of *Platygaster*), in which the endoparasitic life of the embryo and larva has essentially modified the course of the development.

F. Transition forms between the two types of development of the Germ-band.

Coleoptera. The germ-band of the Coleoptera, which, like that of the Hymenoptera, does not attain to any great length, shows in its anterior and principal portion (Fig. 144, *k*) the characters of a germ-band grown over by the embryonic envelopes. It is superficial and is grown over by the forward extension of a caudal fold (*af′*) and paired cephalic folds (*af*) (Fig. 134 *C*, *af″*, p. 270), which soon fuse, to which are added, in *Lina* (GRABER, No. 30), lateral folds that arise independently. The posterior end of the germ-band, on the contrary, develops entirely according to the invaginating type described in connection with the *Libellulidae*. In *Hydrophilus* (KOWALEVSKY, No. 48, and HEIDER, No. 38), at the posterior end of the rudiment of the germ-band, there is a pit (Fig. 134 *A*, *g*, p. 270) which exactly corresponds to the invagination known by authors as the germ-prominence (p. 276). As this pit deepens, the most posterior end

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* [BÜRGER (No. II.) has published a full account of the embryology of this bee, based upon CARRIÈRE's notes. He finds only one envelope arising from the peripheral portion of the blastoderm and persisting for a short time.—ED.]

of the germ-band develops (Fig. 144, *k'*), bends round dorsally, and sinks into the yolk. The most posterior part of the germ-band is thus here immersed; the anal end is directed forward and applied to the dorsal side of the egg; in short, it shows all the characters of the invaginated germ-band (Fig. 144, *k*).

The germ-band, in the Coleoptera, is thus originally bent round dorsally over the posterior pole of the egg. The cephalic end of the germ-band accordingly lies at first some distance from the anterior pole (Fig. 134 *D*, p. 270). It, however, gradually moves towards the anterior pole (Fig. 134 *E*), while the posterior end moves back from its dorsal situation to the posterior pole. This shifting causes the posterior invaginated portion of the germ-band to be, as it were, drawn out of the yolk, so that, finally, the germ-band throughout its whole length is superficial. This shifting of the germ-band corresponds exactly to the process of rotation. In *Hydrophilus*, however, the rupture in the embryonic envelopes takes place only at a later stage.

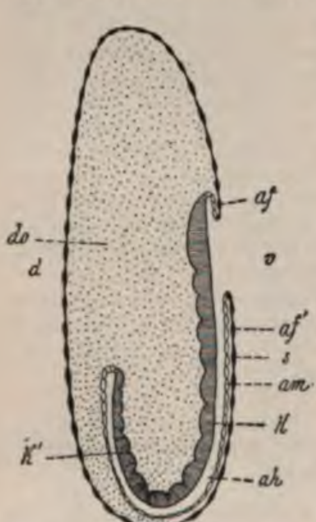

Fig. 144.—Diagram of a median longitudinal section through a *Hydrophilus* embryo in the stage depicted in Fig. 134 *D*, p. 270 (after Heider). *af*, anterior amniotic fold; *af'*, posterior amniotic fold; *ah*, amniotic cavity; *am*, amnion; *do*, food-yolk; *k*, the segmented germ-band, which is already bilaminar; *k'*, posterior end of the germ-band bent round dorsally and sunk into the yolk; *v*, ventral side of the egg; *d*, dorsal side of the same.

Conditions like those just described for *Hydrophilus* are found in the other Coleoptera, as may be gathered with special distinctness from the observations of Graber (No. 30) on *Lina* and of Wheeler (No. 95) on *Doryphora*. Here also the posterior end of the germ-band is bent in dorsally and sunk into the yolk. The principal difference between these cases and that of *Hydrophilus* is found in the fact that the cephalic end of the band appears from the first near the anterior pole of the egg, and consequently the movement accompanying rotation is not here to be observed.

We have already pointed out (p. 284) that the posterior end of the germ-band in the Diptera is sunk into the yolk, in the same way if not to the same extent as in the Coleoptera. We have here also the last indications of the formation of a germ-band by invagination. The presence of these vestigial conditions, and above all the condition of *Hydrophilus* (and *Oecanthus*) seem to indicate that the formation of the germ-band by invagination is the primitive method in the group of Insecta, while the growth over it of the amniotic fold represents a secondary condition (Will, No. 97). The movement of rotation which can be observed in *Hydrophilus* and *Oecanthus* is only comprehensible on this assumption.

G. General Considerations.

We have seen above (Figs. 113, p. 226, and 114, p. 227) that, in the Myriopoda, the germ-band, as it increases in length, is flexed ventrally and sinks into the interior of the egg. In this invagination, which we must imagine to have come about at first through the difficulty of accommodating the long germ-band within the spherical egg, we shall have to seek (as GRABER, No. 149, indicated, and WILL, No. 97, more recently proved in greater detail) the starting-point for the development of the invaginated germ-band of the *Libellulidae*. We shall therefore consider the invaginated form of germ-band as the most primitive in the Insecta. A careful comparison between the condition of the Myriopoda and that of the *Libellulidae*, indeed, reveals certain differences. In the Myriopoda, the germ-band alone is drawn into the invagination. In the *Libellulidae*, on the contrary, in which the germ-band is comparatively short, it occupies only one side of the depression, while the opposite side seems to be occupied by a part of the blastoderm which has been drawn into the depression with the band, and is then known as the amnion. The part of the blastoderm not concerned in the formation of the germ-band in this case therefore is more extensive, and this marks the first commencement of the formation of the embryonic envelopes.

In the Myriopoda, the parts of the germ-band not drawn into the depression remain simply uncovered. In the *Libellulidae*, on the contrary, they are grown over by a fold (amniotic fold) which arises secondarily. This formation of folds is a new acquisition in the Insecta by which the system of embryonic envelopes is completed. It is contrasted by WILL (No. 97), as the *secondary* part of the embryonic envelopes, to the *primary* part which arises by invagination. We should, however, hesitate to lay much stress upon this distinction.

In the more highly developed and specialised Insect types, the secondary formation of folds becomes more prominent, while the development of the germ-band through invagination sinks into the background. The germ-band grown over by the amnion is thus derived from the invaginated band, and the development of the former marks an ontogenetic advance, as the complicated process of rotation is now eliminated.

The cases of vestigial development of the embryonic envelopes which have been observed in endoparasitic eggs (*Pteromalina*, *Tachinidae*), in the eggs of the viviparous *Cecidomyiidae*, and in the *Muscidae* must be regarded as secondarily acquired, when we take into consideration the condition of other nearly related forms.

We have as yet no certain data to help us in discussing the question of the physiological significance of the germ-envelopes. Although the increase of the yolk-absorbing surface may have been of importance for the development of the invaginated germ-band, this consideration does not help to explain the development of the amniotic folds that have grown over the germ-band. In the latter we seem to see the influence of an ontogenetic tendency which led to the germ-band being separated from direct contact with the inner surface of the chorion (or vitelline membrane). This may have afforded greater protection against certain mechanical injuries, perhaps also against the danger of desiccation or adherence. The latter hypothesis seems to receive special support from the fact that eggs with degenerated embryonic envelopes (*Ceridomyia*, *Tachina*, *Muscidae*) are, in consequence of the nature of their surroundings, less exposed to this danger. All these conjectures, however, afford little satisfaction.

4. Development of the external form of the Body.

A. Segmentation.

The first traces of segmentation are found very early in the germ-band of the Insecta, which becomes divided up by superficial transverse furrows into a number of somites. This segmentation, in the form of consecutive metameres, may appear as early as the very beginning of gastrulation (*Hydrophilus*, Kowalevsky and Heider, Fig. 134 *A* and *B*, p. 270, and *Chalicodoma muraria*, Carrière, No. 13, Fig. 156, p. 315). The transverse boundaries of the segments then extend not only over the middle plate (p. 310), from the invagination of which the lower germ-layer arises, but laterally over the lateral plates (Fig. 156, *s*), which become the ectoderm of the germ-band. These transverse furrows owe their origin to the alternate thickening and thinning of the epithelium, which at this stage forms the embryonic rudiment, the furrows corresponding to the thin areas. It follows that, in the forms just enumerated, after gastrulation has taken its course, not only the ectoderm, but the lower layer also, is segmented.

Heider (No. 38) maintained in the case of *Hydrophilus* that the first indications of segmentation even precede gastrulation. Similar transverse zones of the blastoderm have been observed by Wheeler (No. 95) in *Doryphora* and by Graber (No. 30) in *Lina*, but these authors interpret them in another way not connected with the later segmentation.

Such an early appearance of segmentation as that found in *Hydrophilus* and *Chalicodoma* must be regarded as a modification of the ontogenetic processes founded on heterochrony. We shall have to regard as primitive the condition found in other forms (*e.g.*, *Lina* and *Stenobothrus*, Graber, No. 30), in which the gastrulation and the separation of the lower layer take place in the unsegmented germ-band, and the division into segments only occurs at a later stage (Fig. 145). In these forms the segmentation is principally noticeable in the invaginated lower layer, although probably, in all cases, the ectoderm also is affected by it at an early stage.

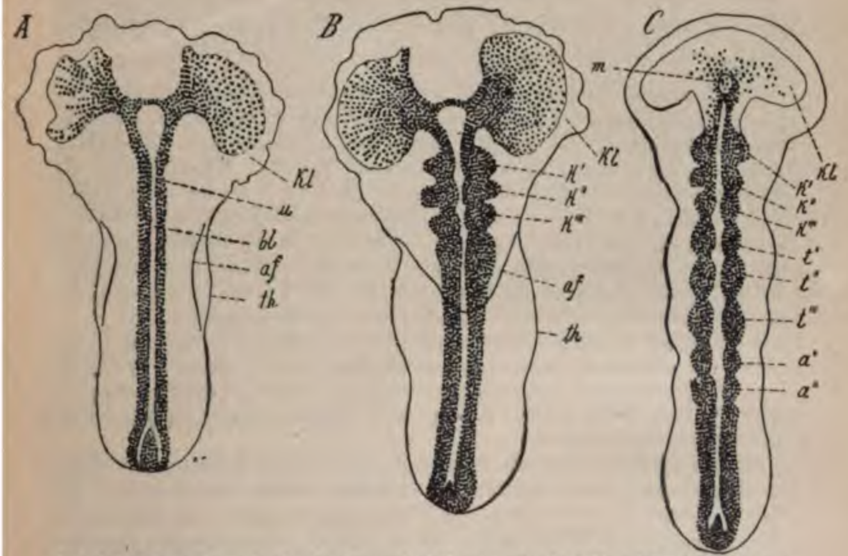

Fig. 145.—Three stages in the development of the germ-band of *Lina* (after Graber). *A*, unsegmented germ-band; in *B* and *C*, the segmentation is recognisable in the lower layer. *B*, with the rudiments of the mandibular and two maxillary segments, to which, in *C*, the three thoracic segments and the two anterior abdominal segments are added. *a'*, *a''*, first and second abdominal segments; *af*, amniotic fold; *bl*, blastopore; *k'*, mandibular segment; *k''*, *k'''*, the segments of the two maxillae; *kl*, cephalic lobes; *m*, mouth; *t'*, *t''*, *t'''*, first, second, and third thoracic segments; *th*, extension of the germ-band in the thoracic region; *u*, lower layer.

In the completely segmented germ-band of the Insect (Fig. 134 *E*, p. 270, and Fig. 146 *A*, p. 295) we distinguish two peculiarly-shaped regions, one corresponding to the anterior end and another corresponding to the posterior end. The anterior or primary cephalic region carries the oral aperture, and is characterised by its great lateral extensions, the cephalic lobes (Figs. 134, *k* and 145, *kl*), while the posterior terminal section, the so-called anal segment or telson, carries the anal aperture (Fig. 146 *A*, *a*). Between these two regions lies the segmented primary trunk-region, which, in the Insecta, seems without exception to consist of sixteen segments. The three anterior of these segments represent the mandibular and the two maxillary segments, which are later drawn into the formation of the head (Fig. 146, *md*, mx_1, mx_2), while the three following develop into the permanent thoracic segments (p_1, p_2, p_3), so that ten segments (besides the telson) must be reckoned as belonging to the posterior or abdominal region of the body.

Ten abdominal segments together with a telson seem typical throughout the group of the Insecta. This number has been observed recently in the germ-band of *Hydrophilus* by Heider, and in various forms (*Lina*, *Stenobothrus*, various Lepidoptera, and *Hylotoma*) by Graber (No. 30). Wheeler (No. 95), Cholodkowsky (No. 19), and Carrière (No. 13) have all made similar observations. In the later stages of embryonic development, this number is apparently in a few forms decreased to nine, the tenth abdominal segment fusing with the telson. This appears to be the case in *Hydrophilus* and *Lina*; in the Lepidoptera, according to Graber (No. 30), a fusion of the ninth and tenth abdominal segments takes place, the telson remaining independent.

With regard to the *primary cephalic region*, it should be mentioned that, taking into account the segmentation of the brain recently observed by Patten (No. 67) and confirmed by several other authors, it has to be assumed that this region is composed of several (three) fused segments (*cf.* pp. 325–328 on the development of the brain).

Another point to be noted is that, according to the statements of various authors, among whom Wheeler and Carrière deserve special mention (the former in connection with *Doryphora*, No. 95, and the latter with *Chalicodoma*, No. 13), a slightly developed and transitory segment, the so-called *pre-maxillary segment*, is intercalated between the primary cephalic region and the first body-segment proper (which represents the mandibular segment). According to Carrière, this structure represents a vestigial pair of limbs and a corresponding pair of ventral ganglia. The latter is said to be concerned in the formation of the circum-oesophageal commissure.

The cephalic lobes usually appear very early (Fig. 145, *kl*). Even when the germ-band is still altogether devoid of segmentation, the primary cephalic region is already characterised by the extensions of the cephalic lobes. A slight broadening can also often be observed in that part of the still unsegmented germ-band which corresponds to the later thoracic segments (Fig. 145 *A* and *B*, *th*). Indeed, Ayers (No. 1) was able to distinguish in the still unsegmented germ-band of *Oecanthus* a primary cephalic region, a maxillary, a thoracic, and an abdominal region, these later regions of the body being indicated by variations in the bulk and breadth of the germ-band. It is on these first rudiments of the body-regions, which are only recognisable as wavy swellings of the lateral contour of the germ-band, that Graber (Nos. 26 and 30) founds his view of the *primary segmentation of the Insectan germ-band*.

According to Graber, the law of the development of the body-segments from before backward, which has been accepted on the whole for the Arthropoda and was specially insisted upon by Balfour, does not apply to the Insecta. In this group the germ-band is said to break up at first into macrosomites, *i.e.*, the slightly indicated swellings of the germ-band recognised by Ayers and corresponding to the permanent regions of the body. The macrosomites are said, by means of a secondary segmentation, to break up into microsomites (the later body-segments). This peculiar type of segmentation, which deviates from that of the other Arthropoda, is to be regarded as inherited from a hypothetical racial form. We, however, are not able to accept this view. Apart from the fact that in *Hydrophilus* (Heider), *Chalicodoma* (Carrière, No. 13), *Mantis* (Viallanes, No. 84), and *Xiphidium*, one of the *Locustidae* (Wheeler, No. 94), there is no sign of any breaking up into macrosomites preceding definitive segmentation, it appears to us that the broadening of the germ-band at the part where later the thoracic region develops may be traced back merely to an accumulation of plastic material, and that it should not therefore be regarded as the expression of a true segmentation. If the lower layer were also affected by this apparent breaking up into macrosomites, the case would be different. Such a condition was actually stated by Graber to exist in *Stenobothrus* (No. 26). From his more recent publication (No. 30), however, it appears that the formation of macrosomites in the lower layer in *Stenobothrus* is not quite distinct. We have therefore only the statements of Nusbaum (No. 59) in connection with *Meloe* and, as no division into macrosomites is found in *Hydrophilus* and *Lina*, the point seems to require reinvestigation.

As a rule, the development of the body-segments in the germ-band of the Insecta takes place from before backward. This has recently been observed, especially by Graber (No. 30), in various forms (*Stenobothrus*, *Hylotoma*, *Lina*). In *Lina*, for instance, the mandibular and the maxillary segments (Fig. 145 *B*, *k*′–*k*″) develop first, and in the next stage the three thoracic segments and the two anterior abdominal segments are added (Fig. 145 *C*), while the other abdominal segments only develop later. In other cases, the development of the segments seems to proceed more equally along the whole length of the germ-band. Our knowledge is, however, very incomplete on this point. An exception to the rule is afforded by *Hydrophilus*, in which the development of the segments of a middle region is somewhat retarded, while the anterior and posterior parts of the germ-band develop more rapidly. In *Pieris*, according to Graber (No. 30), the thoracic segments precede all the others in development. The maxillary segments soon follow, and finally the abdominal segments form.

B. Stomodaeum and Proctodaeum. Labrum.

After the segmentation of the germ-band is completed, the next ontogenetic changes to be remarked are the development of the stomodaeum and the proctodaeum and the rudiments of the limbs. The fore-gut and the hind-gut appear as ectodermal invaginations, the stomodaeum and the proctodaeum, in the primary cephalic region and on the telson (Figs. 145 *C*, *m*, and 146 *A*, *m* and *a*). As a rule, the stomodaeum begins to develop a little earlier than the proctodaeum in the Insecta (Fig. 145 *C*, *m*). To this rule, however, the *Muscidae* form an exception, if the observations of **Voeltzkow** (No. 85) and **Graber** (No. 28) as to the early appearance of the proctodaeal invagination in these forms are confirmed.

About the time when the stomodaeal invagination appears, and anterior to it in position, a forward swelling of the anterior edge of the primary cephalic region is to be remarked. This is the so-called *procephalon* (Fig. 146, *vk*), which represents the common rudiment of the *labrum* and the *clypeus*. In many cases, this rudiment first appears in the form of a small paired prominence (Fig. 160, *l*, p. 326), which gives rise later, by fusion in the median line, to an unpaired swelling which is still somewhat indented at the middle. This is the case in the Coleoptera (*Hydrophilus*, **Kowalevsky**, **Graber**, No. 25, and **Heider**; in *Lina*, **Graber**, No. 30; in *Meloe*, **Nusbaum**, No. 63; in *Acilius*, **Patten**, No. 67), in the Lepidoptera (**Tichomiroff**, No. 79, and **Graber**, No. 30), in *Chalicodoma* (**Carrière**, No. 13), and in other forms. The rudiment is, on the contrary, originally single in *Apis* (**Grassi**, No. 32), in *Blatta* (**Cholodkowsky**, No. 19), and in *Mantis* (**Viallanes**, No. 84). The rise of the procephalon which, by many authors, is called simply the labrum, from a paired rudiment has repeatedly led to its being compared with a pair of pre-oral appendages, but the grounds for such a comparison are, as we think, insufficient. This view has been adopted recently by **Patten** (No. 67), who described the procephalon simply as the first pair of antennae, and also by **Carrière** (No. 13). The labrum of the Insecta seems to us to find its homologue in the structures called by the same name in other Arthropoda (especially in the Crustacea), to which the interpretation just mentioned would be inapplicable.

It should be mentioned that, in the early embryonic stages of many Insects, a provisional lower lip, arising from a paired rudiment, is found just behind the mouth. This is not to be confounded with the permanent lower lip of the Insecta, which arises by the fusion of the second pair of maxillae. The provisional lower lip was first observed by **Bütschli** (No. 11) in *Apis*, and called by him the inner antennae; it was found later by **Tichomiroff** in the Lepidoptera. **Heider** described it as the "lateral oral lips" in *Hydrophilus*, and it has recently been observed by Nusbaum (No. 63) in *Meloe*. This structure may best be compared with the paragnatha of the Crustacea, although we are apparently precluded from homologising it with this latter.

C. Extremities.

The limbs appear as sac-like swellings of the surface of the segments, which, as a rule, are directed backward. The antennal rudiments must be regarded as the most anterior pair of true limbs; this belongs to the cephalic region, and arises near the posterior edge of the cephalic lobes, at the point where these pass into the mandibular segment (Figs. 146, *an*, and 147, *at*). It should be specially pointed out that the antennal rudiment, even when it first appears, is, as Weismann (No. 87) has shown, post-oral in position (Fig. 147, *at*) and shifts towards the mouth only later, finally coming to lie in front of or above it. The antennal rudiment, in its external appearance, development, and position closely resembles the other limb-rudiments.

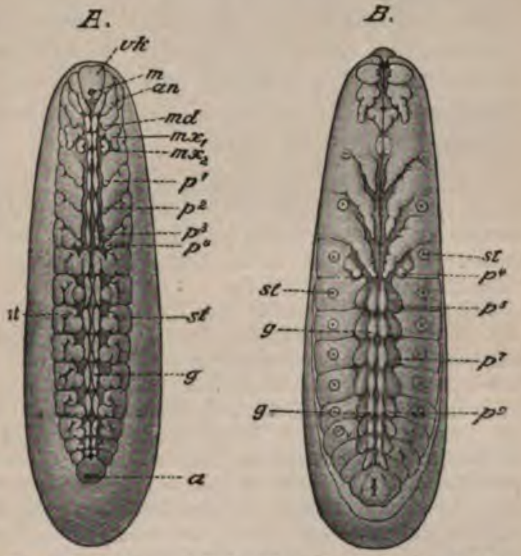

Fig. 146.—Embryos of *Hydrophilus* with limb-rudiments (after Heider, from Lang's *Text-book*). *a*, anal aperture; *an*, antenna; *g*, rudiment of the ventral chain of ganglia; *m*, oral aperture; *md*, mandible; mx_1, first, mx_2, second maxilla; p^1, p^2, p^3, the three pairs of thoracic limbs; p^4, p^5, p^7, p^9, rudiments of the first six abdominal limbs; *st*, stigmata; *vk*, procephalon.

Weismann's important discovery that the antennal rudiment is originally post-oral in position has recently been confirmed by various observers (Graber, No. 25, and Heider, No. 38, for *Hydrophilus*; Patten, No. 67, for *Acilius*; Graber, No. 30, for *Stenobothrus*, Lepidoptera, *Hylotoma*; Nusbaum, No. 63, for *Meloe*; Wheeler, No. 95, for *Doryphora*; Carrière, No. 13, for *Chalicodoma*, etc.). This position, as well as the agreement in form between the antennal rudiment and the other limbs, lends important support to the view we have already expressed in connection with *Peripatus* (p. 186, etc.), and which also applies to the Insecta, that the antennae are structures secondarily shifted to a position in front of the mouth, and that they are entirely homonomous with the other trunk-limbs, and cannot therefore be traced back to the primary cephalic tentacles of the Annelida.[*]

CARRIÈRE (No. 13) has asserted the presence in *Chalicodoma* of a pre-antennal limb-rudiment. According to him, the rudiment of the procephalon represents a first pair of limbs, the pre-antennal rudiment the second, the antennae the third, the transitory limb of the hypothetical pre-maxillary segment (p. 292) the fourth, and the mandible the fifth pair of the series. These statements require confirmation before we can accept them as explaining the true relationship of the series of the limbs.

Of the limb-rudiments following the antennae, the three next pairs are transformed into the *jaws* (mandibles, first and second maxillae, Figs. 146 and 147, md, mx_1, mx_2). These rudiments develop early and with a complicated form in keeping with their later specialisation, the mandibles appearing toothed and the maxillae lobed. The second maxillae fuse together in later stages to form the lower lip. The three pairs of limbs which follow these (the *thoracic legs*, Figs. 146 and 147, p^1, p^2, p^3,) exhibit a massive development, the first traces of the future segmentation soon becoming apparent on them.

In the *Libellulidae*, the rudiment of the second maxilla appears very large in the embryo (Fig. 138, mx^2, p. 278), so that it looks more like that of a thoracic limb than like those of the other jaws. Its special development is probably connected with the size attained by the lower lip (mask) of the larva which proceeds from it (p. 359).

With regard to the order of appearance of the different limbs, our knowledge is as yet somewhat incomplete. Here also we find repeatedly that the general order of development is, according to the ontogenetic law, from before backward. In many forms the antennal rudiments seem to be the first to appear, while the maxillary rudiments and those of the legs all develop simultaneously, but somewhat later than the antennae. This is the case in *Hydrophilus*, *Melolontha*, and *Stenobothrus*. In *Lina*, according to GRABER (No. 30), the mandibles precede the antennae. Among the *Libellulidae*, according to BRANDT (No. 7), the rudiments of the thoracic limbs appear first, then those of the maxillae, and only later those of the antennae. In those Insects whose larvae are limbless, on the contrary, the rudiments of the thoracic limbs appear late and in an arrested condition (*Apis* and *Chalicodoma*), or are altogether suppressed (*Muscidae*). In the first case, the limb-rudiments degenerate before the larva hatches. It would be interesting to trace the relation of these degenerating rudiments to the imaginal discs of the thoracic limbs that develop later, concerning which, as far as we know, no statements have been published.[†]

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[*] From this point of view, the malformation observed by KRIECHBAUMER in *Bombus* (*Entomol. Nachr.*, Jg. XV.) is not without interest; an antenna was by this author found deformed so that it resembled a leg, and at its end carried two well-developed claws. See BATESON, *Materials for the Study of Variation*, p. 146.

[†] [BÜRGER (No. II.) finds in *Chalicodoma* that the thoracic appendages of the embryo flatten out and their hypodermal cell-layer thickens and becomes the imaginal discs of the thoracic limbs of the adult.—ED.]

Soon after the appearance of the thoracic limbs, rudimentary appendages can be seen on the *abdominal segments* also (Figs. 136 p_4, p_9, and 137 *A*, a_1–a_8). These, in most cases, exactly correspond in position and in the manner of their development to the limb-rudiments of the preceding segments, so that we may consider them as fully equivalent to the latter. The first statements as to the presence of limb-rudiments on the first abdominal segments were made by Rathke (for *Gryllotalpa*), and the first mention of the presence of limb-rudiments on all the abdominal segments by Bütschli (No. 11, *Apis*). These statements have recently repeatedly been verified in numerous Insects (for the literature on this point see especially Graber, Nos. 25 and 30, Wheeler, No. 91, and Carrière, No. 15). The first point to be noted is, as Graber has shown, that, in the Orthoptera and Coleoptera, as well as in some Hemiptera, the appendages of the first abdominal segment, as compared with those of the subsequent segments, are more massive and in later stages develop characters peculiar to themselves, while, in the Lepi-

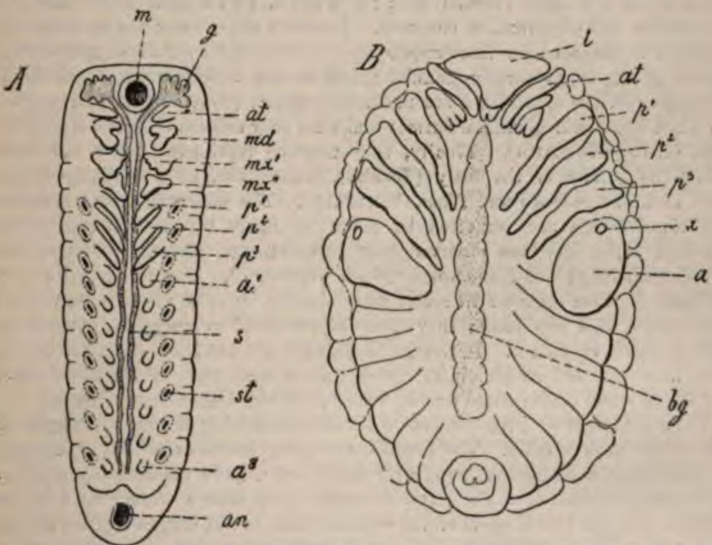

Fig. 147.—Two stages in the development of the germ-band of *Melolontha* (after Graber). *A*, stage with eight pairs of abdominal limb-rudiments (a^1–a^8). *B*, older stage; the germ-band is very much broadened. a^1, limb belonging to the first abdominal segment (in *B*, widened out into a sac); a^8, limb belonging to the eighth abdominal segment; *an*, anus; *at*, antenna; *bg*, ventral chain of ganglia; *g*, brain; *l*, labrum; *m*, mouth; *md*, mandible; *mx'*, first, *mx''*, second maxilla; p^1, p^2, p^3, first, second, and third thoracic limb; *s*, lateral strand of the ventral nerve-cord; *st*, stigma; *x*, point of attachment of the sac-like first abdominal limb.

doptera and Hymenoptera, the limb-rudiments of the first abdominal segment are, in some cases, less developed than those of the other segments, and in no case do they attain a greater development.

In the Orthoptera and Coleoptera, the limb-rudiments of the first abdominal segment show, as is often the case with vestigial organs, considerable variability in their later development. They are most leg-like in *Mantis*, according to GRABER, and in this genus, as well as in some other forms, they even show signs of segmentation, the finger-like process appearing divided into two by a transverse constriction. The limb-rudiments of this segment in *Melolontha* attain an altogether excessive development (Fig. 147 *B*, a^1, GRABER), being transformed into large vascular sacs, the walls of which seem to be composed of massive coarsely-granular elements. In many other cases a glandular significance is suggested for these appendages, the walls at their distal parts being formed of very large coarsely-granular glandular cells which are often pigmented. In such cases, the appendages are mushroom-shaped (*Gryllotalpa*, *Hydrophilus*) or, when the distal glandular surface sinks in, they assume the form of stalked cups (*Meloe*, NUSBAUM). Finally, they may be represented by a sac sunk below the surface of the body (*Tenebrio*, CARRIÈRE), or a similarly-shaped solid structure (*Cicada* and *Nepa*, WHEELER). The different shapes assumed by this structure are connected by means of many transition forms. The secretion which has been observed may be gelatinous (*Meloe*, NUSBAUM, and *Cicada*, WHEELER) or filamentous (*Nepa*, WHEELER). The physiological significance of these organs still seems very obscure, in spite of the observations which have been published; they have been claimed as embryonic respiratory organs (gills) or glands. It should be pointed out that the character of the cells here regarded as glandular agrees closely with that of the elements of the dorsal organ (invaginated serosa) before the latter begins to disintegrate.

The appendages we have just been discussing invariably degenerate completely before the larva hatches. The same is, as a rule, the case with the appendages of the posterior abdominal segments, which are usually considerably smaller. It is possible that when the latter disappear they take a certain part in the formation of the lateral parts of the ventral plate, as was conjectured by HAASE (No. 153) when reviewing the condition of *Machilis* and *Blatta*, and as was more recently rendered probable by GRABER (No. 30) for *Melolontha*.

With regard to the development of the abdominal extremities (*pedes spurii* or *prolegs*) of the caterpillars of the Lepidoptera and the caterpillar-like larvae of the *Tenthredinidae*, it appears from the researches of KOWALEVSKY (*Sphinx*), TICHOMIROFF (*Bombyx*), and GRABER (No. 30, *Bombyx* and *Hylotoma*) that limb-rudiments first form on all or most of the abdominal segments, but that they very soon disappear on those segments which, in the larva, have no limbs, while on the other segments they are transformed into the functional prolegs. To this view the observations of GOOSSENS and KNATZ, according to which single pairs of these prolegs first develop during larval life, are apparently unfavourable. We should here have to suppose, as GRABER (No. 30) also has pointed out, an embryonic rudiment remaining for a considerable time in a latent condition. On the whole, the embryological data seem to support the view of BALFOUR, which CHOLODKOWSKY has recently adopted, and to which GRABER (No. 30) is inclined, that the abdominal appendages of the caterpillars of the Lepidoptera and Hymenoptera are to be regarded as true limbs. We have already had several examples in the Crustacea of the disappearance and re-development of a limb out of a rudiment which has meantime been latent (mandibular palp of the Decapod larva, Vol. ii., p. 312, maxillipedes of the Stomatopoda, Vol. ii., p. 300). A similar example is afforded among the Insecta by the thoracic limbs of many Hymenoptera; these appear as rudiments in the embryo, disappear later, and reappear in the imago.* The same process will be found to explain the phylogenetic appearance of the abdominal limbs of the caterpillars and Tenthredinid larva; for it can hardly be doubted that the Lepidoptera and the Hymenoptera, as well as all Heteromorpha, are to be derived from homomorphous ancestral forms which, in the larval condition, were devoid of abdominal limbs. The larval form of the caterpillars, in spite of its apparent resemblance to *Peripatus*, must be accepted as a secondary ontogenetic condition acquired in adaptation to certain conditions of life (p. 366).

Special mention should be made of the appendages of the last abdominal segment (anal or terminal segment, which in many orders of Insects, especially in the lower orders (Orthoptera genuina, *Ephemeridae*, Odonata, Plecoptera), persist throughout life as the so-called *cercopoda* (*cerci*). It must still be considered doubtful, on account of the nature of the terminal segment, whether we may consider these appendages as the equivalents of the other true limbs. According to the observations of CHOLODKOWSKY (No. 19), their development in *Blatta* seems to support such a view. They here appear not only in a form resembling that of the other abdominal appendages, but a process of the coelomic sac which develops in the terminal segment extends into them as into the other limb-rudiments. The homologue of the cerci is perhaps found in the posterior extremities of the Lepidopteran caterpillar, which lie beneath or near the anus, the so-called *anal prolegs* which, according to GRABER (No. 30), develop on the terminal segment. The three-jointed anal cerci of the Tenthredinid genus *Lyda* and the structure known as *anal spikes* in other forms (*Nematus*, ZADDACH, and *Hylotoma*, GRABER, No. 30) correspond to them. The so-called anal prolegs of the larvae of many *Tenthredinidae* are, on the contrary, appendages belonging to the tenth or penultimate abdominal segment.

There is a certain relation also between the typical abdominal limb-rudiments and the unjointed appendages of the ventral plate of the ninth abdominal segment, known as the *styli*; these are found in many Orthoptera, and persist throughout life in the males. According to CHOLODKOWSKY (No. 19), they are derived in *Blatta* from the embryonic limb-rudiment of this segment. HAASE (No. 153), on the contrary, will not allow that either the appendages under consideration or those small movable processes found on the abdominal segments of the Thysanura (ventral stylets) have the morphological significance of true limbs, but regards them merely as the equivalent of the coxal spurs of *Scolopendrella*.

We are here led to ask to what extent the external genital appendages, the so-called gonapophyses, are to be traced back to limb-rudiments. The researches of KRAEPELIN and DEWITZ (No. 103) have revealed that the ovipositors of the Hymenoptera and the Locustidae, and the corresponding genital appendages of the male in these forms, are derived from imaginal discs of the eighth and ninth abdominal segments, which, when they first appear in the larva, closely resemble those imaginal discs of the larva of *Corethra*, which yield the thoracic limbs (p. 371). BÜTSCHLI (No. 11) and others have therefore attempted to refer the gonapophyses of these forms to true abdominal limb-rudiments. In support of this assumption, we might point out that these imaginal discs

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* [See footnote, p. 296.—ED.]

develop from the abdominal limb-rudiments present in the embryo. It should, however, be mentioned that **Haase** (No. 153), following **Uljanin**, has recently opposed this view, although, as it appears to us, with insufficient reason, maintaining that the gonapophyses should be regarded merely as secondarily-acquired external appendages.*

We cannot deny that a certain phylogenetic significance attaches to the presence in the Insect embryo of abdominal limb-rudiments that degenerate later. Considering the near relationship that exists between the Insecta, the Myriopoda, and *Peripatus*, we must see in the appearance of these rudiments the ontogenetic recapitulation of the conditions belonging to an ancestral form of the Insecta, in which all the body-segments were still provided with well-developed pairs of limbs resembling the present thoracic limbs. We should have to attach a certain importance to the fact that, in the Orthoptera, the embryonic limb-rudiments of the first abdominal segment are always more developed than those of the following segments and, in *Mantis*, exactly resemble legs. Since, in *Campodea* (**Haase**, No. 153), a true rudiment of a leg is retained on this segment, we are justified in raising the question whether, in the degeneration of the abdominal extremities in the series of ancestors of the Insecta, the hexapod condition was not preceded by an octopod condition. This would explain the fact that the segment in question, in many points of its development, resembles the thoracic rather than the abdominal segments.

The limb-rudiments which are found as sac-like bulgings of the surface of the germ-band are from the commencement of their development filled with mesoderm. In most Insects there is at first no arrangement in the mesodermal cells that enter the limb-rudiments, but the Orthoptera seem more nearly to follow the Myriopoda and *Peripatus*, in so far as, in them, diverticula of the coelom extend into the rudiments (**Cholodkowsky**, No. 19; **Graber**, Nos. 26 and 30).

D. Nervous System and Tracheal Invaginations.

The rudiments of these two systems of organs help essentially to *determine the external form* of the Insectan germ-band. The rudiment of the nervous system usually appears very early, before the limb-rudiments are recognisable. We find, as rudiments of the ventral

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* [**Heymons** (Nos. XVI. and XXII.) has investigated the development of the cerci, gonapophyses, and stylets in *Lepisma* and other Insects, and he concludes that the cerci are true appendages, that the styles appear to be dermal processes replacing true appendages and intimately related to them, and that the gonapophyses have no relation to appendages. **Wheeler** (No. XLIV.), on the other hand, is strongly in favour of regarding the gonapophyses as modified abdominal appendages. **Uzel** (No. XL.) regards the ventral stylets of *Campodea* as direct derivatives of abdominal appendages.—**Ed.**]

chain of ganglia, two swellings running longitudinally along the germ-band near the median line (*primitive swellings*, Fig. 147 *A*, *s*) and a channel lying between them (*primitive groove*, *neural groove*). Segmentation takes place early in the primitive swellings, broader parts (rudiments of the ventral ganglia) alternating with constricted parts (longitudinal commissures) in regular segmental order (Fig. 146 *A*, *g*). Anteriorly, the primitive swellings diverge from one another, as the circum-oesophageal commissures, and pass directly into the cephalic lobes. Here each passes into the brain-rudiment, a somewhat large ectodermal thickening, the shape of which will be described more in detail below (p. 326). The rudiment of the brain and that of the ventral chain of ganglia are thus, in the Insecta, connected from their first appearance.

The *tracheae* arise as ectodermal invaginations recurring in each segment (Fig. 146 and 147, *st*). The apertures of the invaginations afterwards become the stigmata. The tracheal invaginations occur regularly on the first to eighth abdominal segment. In the thorax, in which the presence of a pair of such invaginations in each segment may no doubt be assumed as the primitive condition, there is variation in this respect in the different groups. In the Lepidoptera, one tracheal invagination appears in the pro-thorax, while none is found in either the meso- or the meta-thorax. The embryos of most Coleoptera and Hymenoptera (*Apis*, BÜTSCHLI, *Hylotoma*, GRABER, No. 30), on the contrary, have no tracheal rudiment in the pro-thorax, but possess such a structure on both the meso- and meta-thorax. The same is the case in the embryo of *Mantis* (GRABER, No. 30).

The tracheal invaginations as a rule develop only after the appearance of the limb-rudiments. An exception to this rule is afforded by *Apis*, in which the tracheal invaginations appear in the thoracic region before the belated limb-rudiments. As a rule the invaginations appear almost simultaneously, only rarely is there any indication of the order of development from before backward. In *Hydrophilus*, for instance, the meso-thoracic stigma appears somewhat earlier than the stigmata of the other segments (GRABER, No. 25).

In the Coleoptera, structures conjectured by HEIDER (No. 38) and WHEELER (No 95) to be the vestiges of tracheal invaginations have been observed on the ninth and tenth abdominal segments.

It should be mentioned here that certain ectodermal invaginations appearing in the head have been regarded as tracheal formations which have lost their primitive function and become secondarily modified. CARRIÈRE (No. 13) following MOSELEY and PALMEN (No. 161) has thus regarded the salivary glands and the tentorial invaginations as modified tracheae. Others (BÜTSCHLI, GRASSI) have considered the Malpighian vessels to be of the same type as the tracheal invaginations. We shall further on give our reasons for not adopting this view.

E. Transition to the Definitive Form of Body.

The development of the definitive shape of the body is accomplished through the circumcrescence of the whole of the nutritive yolk by the germ-band. We have seen above (p. 272) that, in the later stages of development, the germ-band as a rule lies in such a way that its anterior end corresponds to the anterior pole of the egg, and its posterior end to the posterior pole. As the germ-band grows considerably in breadth, its lateral edges shift up dorsally over the surface of the food-yolk (Figs. 150 *A–F*, 169, 170, 171, and 172). In this way the lateral parts, and later the dorsal parts, of the larval body are formed. By means of this circumcrescence, the food-yolk comes to lie entirely within the embryo, and finally fills the lumen of the archenteron (Fig. 150 *F*). The closing of the larval body dorsally through the circumcrescence of the food-yolk by the germ-band is so intimately connected with the degeneration of the embryonic envelopes that we shall have to return to these processes later on.

The dorsal parts of the embryo in the cephalic region develop independently of the broadening of the germ-band described above. The segments of this region, *i.e.*, the maxillary, only take part to a small extent in the development of the dorsal portion, the latter being mainly formed by the bending over dorsally and the backward extension of the cephalic lobes as well as of the procephalon. The anterior end of the germ-band is therefore here bent over dorsally. An actual dorsal flexure of the cephalic region develops, as was first pointed out by WEISMANN and later by HATSCHEK and HEIDER (No. 38). During this flexure of the anterior end of the body, the part of the procephalon lying near the mouth appears as a transverse swelling (labrum). The former most anterior part of the procephalon now becomes the clypeus and assumes a more backward position. The cephalic lobes in this process of shifting pass towards the dorsal side, and the antennal rudiments consequently shift in front of or above the mouth.

5. Completion of the dorsal part of the Embryo and degeneration of the Embryonic Envelopes.

In most of the Arthropoda that have so far come under review (Crustacea, Arachnida, Myriopoda, etc.), development takes place through the formation of a so-called germ-band, but without the formation of actual embryonic envelopes. The surface of the whole egg is then covered partly by the band-like embryonic rudiment and partly by the unmodified blastoderm. The dorsal part of the embryo is there formed by the continuous broadening of the germ-band which by its growth, extends over the greater part of the surface of the egg, the region covered by unmodified blastoderm becoming more and more circumscribed. It is as a rule assumed that the latter takes part in the closing of this dorsal region by being transformed histologically to form the ectoderm of the germ-band. It is possible that in these forms also part of this blastoderm gradually degenerates. We have (Vol. ii., p. 150) conjecturally referred the formation of the so-called dorsal organ of certain Crustacea to such a process of degeneration. A similar method of development of the dorsal part of the embryo perhaps also occurs in the *Poduridae*, in which a dorsal organ is found which develops in the early embryonic stages, and is connected with a larval cuticle that envelops the embryo (LEMOINE, No. 51), but in other respects its significance is somewhat obscure (p. 268). In most insects the process is more complicated, in so far as an amniotic fold arises at the junction of the germ-band with the undifferentiated part of the blastoderm, the degeneration of this fold being intimately connected with the completion of the dorsal surface of the embryo.

FIG. 148.—Diagram of the development of the dorsal tube through invagination of the dorsal plate (transformed serosa). Succeeding the stage depicted in Figs. 138 *C* and 140 *D*. *am*, amniotic fold (now forming the provisional dorsal integument); *r*, dorsal tube, which is already commencing to disintegrate.

A very simple case of the formation of the dorsal region in the embryo which, however, we can certainly not regard as primitive, is found in the *Muscidae* and a few other Diptera in which the amniotic fold is incomplete (p. 284). Here (according to KOWALEVSKY, No. 49, and GRABER, No. 28) the amnion is simply flattened out again. The amnion and the serosa then together form a simple epithelium which corresponds to the unmodified part of the blastoderm in the Crustacea, Arachnida, and Myriopoda, and here also seems to take the same part in the development of the dorsal ectoderm. More complicated and very varied methods of formation of the dorsal region and of the involution of the embryonic envelopes are found in the other Insecta, the four following types being distinguishable.

[In *Lepisma*, one of the Thysanura (HEYMONS, No. XVI), the germ-band attains a ventral flexure, and is invaginated into the yolk, in a manner suggestive of the Diplopoda (p. 229), at a very early period. Here, however, a slight amnion forms, and by a narrowing of the cavity of invagination an amniotic cavity arises; the amniotic folds, with the serosa, which latter surrounds the greater part of the egg, however, never unite, so that the amniotic cavity is never closed, and rotation takes place without rupture of the embryonic membranes. The germ-band, commencing at its anterior end, simply emerges from the amniotic cavity through the persistent amnion-pore. The serosa contracts dorsally, becomes invaginated, and forms the dorsal organ or sac, which then disintegrates. This condition is distinctly more primitive than that seen in the *Libellulidae*, and recalls the condition of the germ-band in the Myriopoda. In this connection an important and highly suggestive paper by WILLEY (No. XLV.) should be studied. WILLEY believes that the amniotic cavity of insect embryos was originally a product of invagination of the germ-band, and that this invagination was primarily derived from and associated with a ventral flexure of the embryo. In this respect he differs from HEYMONS, who considers that the dorsal flexure of the Chilopoda and *Poduridae* is primitive, whereas WILLEY would rather regard the ventral flexure of *Lepisma* and the Diplopoda in this light. WILLEY further regards the dorsal organ of the *Poduridae* and the indusium of the *Locustidae* as vestiges of a trophoblast such as occurs in *Peripatus novae-britanniae* (p. 216).—ED.]

A. Involution through the development of a continuous dorsal amnion-serosa sac.

In describing the development of the *Libellulidae* (Fig. 138 *C*, p. 278) we saw that, after rotation had taken place, the embryonic envelopes (the amnion and the serosa) which had grown together, represent a membrane which envelops the dorsal yolk-sac (*am* + *se*). The condition then somewhat resembles that seen in the *Muscidae* after the flattening out of the amniotic fold. In this membrane, the part yielded by the amnion is clearly distinguishable from that yielded by the serosa, for while the serous portion has greatly thickened by continuous contraction to form a *dorsal plate*,* the amnion has retained its character as a delicate flattened epithelium (Fig. 140, *C* and *D*, *am*, *r*, p. 281).

The further fate of the embryonic envelopes in the Libellulidae has not been observed. We can, however, complete our description by reference to other forms which show the same type of development. As development advances, the food-yolk becomes more and more restricted to the interior of the embryo, or more strictly speaking, of the developing enteron. The yolk-sac consequently diminishes in size, and the absorption of the food-yolk into the enteron produces a collapse of the dorsal plate, this latter sinking in and forming a thick-walled sac, the so-called dorsal tube (*dorsal organ*, Fig. 148, *r*). The walls of this sac soon undergo disintegra-

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* The dorsal organ of the Podurid embryo seems to be quite peculiar in its formation, and cannot be referred to the dorsal plate here mentioned, as is shown by its early appearance (LEMOINE, No. 15).

tion; the degenerating serosa-cells lose their epithelial connection, and in this disintegrated condition are absorbed into the intestinal canal with the rest of the food-yolk. Simultaneously with this disintegration, which leads to the complete degeneration of the dorsal organ, the outer aperture of invagination completely closes. In this way the serous part of the wall of the yolk-sac becomes disintegrated. There now only remains the amniotic portion of this wall, which, standing in direct communication with the ectoderm of the embryonic rudiment, represents a provisional dorsal integument. It still appears doubtful to what extent this provisional integument passes over into the permanent wall, *i.e.*, to what extent the amnion is transformed into the definitive hypodermis (a view which **Graber** (No. 27) and others have been disposed to adopt). It would appear very strange if the permanent dorsal integument were to be utilised in earlier embryonic stages as a provisional ventral embryonic envelope (amnion), and as, on the other hand, as we shall show (p. 307), the degeneration of the amnion was directly observed by **Wheeler** in *Doryphora*, we must leave the question open whether, as a rule, in the Insecta, the germ-band alone forms the whole of the embryonic rudiment, and also brings about, by its dorsal extension and subsequent union, the completion of the permanent dorsal integument, while the amnion serves as a provisional integument, which later undergoes gradual absorption.

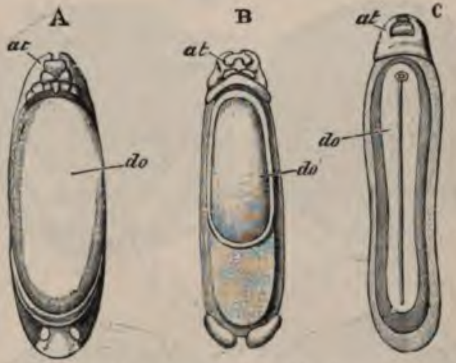

Fig. 149.—Three embryos of *Hydrophilus* from the dorsal side (after **Kowalevsky**, from **Balfour's** *Text-book*). *A*, the serosa has retracted to the dorsal side and has thickened to form the dorsal plate (*do*). *B*, the dorsal plate (*do*) is partly invaginated and covered by the amnion (Fig. 150 *D*). *C*, the dorsal tube is completely developed and opens externally only through an anterior pore (*cf.* Fig. 150 *E*). *at*, antenna; *do*, dorsal organ in various stages of development.

The above-described process of the completion of the dorsal body-wall by the development of a dorsal organ and provisional completion by means of the amnion, probably applies to the *Libellulidae*. It is also found in all Rhyncota (**Graber**, No. 27, in *Pyrrhocoris;* **Metschnikoff**, No. 55, and **Brandt** in

Corixa and *Hydrometra*; also METSCHNIKOFF and WITLACZIL in the *Aphidae*) and in most Orthoptera genuina (*Blatta*, WHEELER; *Oecanthus*, AYERS, No. 1; *Gryllotalpa*, KOROTNEFF, No. 47).

Among the Coleoptera, in which the posterior end of the germ-band arises by invagination, a few forms belong to the type of transformation just described (*e.g.*, *Hydrophilus*, KOWALEVSKY, No. 48, HEIDER, No. 37, GRABER, No. 27; and *Melolontha*, GRABER, No. 27). The only distinction is that here the rupture of the embryonic envelopes takes place only after the completion of the rotation (p. 288), at a time when the germ-band already lies ventrally and is superficial. The fused embryonic envelopes rupture in the median line and draw back to the sides of the germ-band, where they form folds exactly like those at the commencement of their development (Fig. 150 *B*). As these folds bend dorsally over the thickened dorsal plate (*s*, Fig. 150 *D*) and fuse in the dorsal median line, a complete tube is formed lined by the serosa (*dorsal tube*, Fig. 150 *E*), while the amnion provisionally completes the dorsal part of the

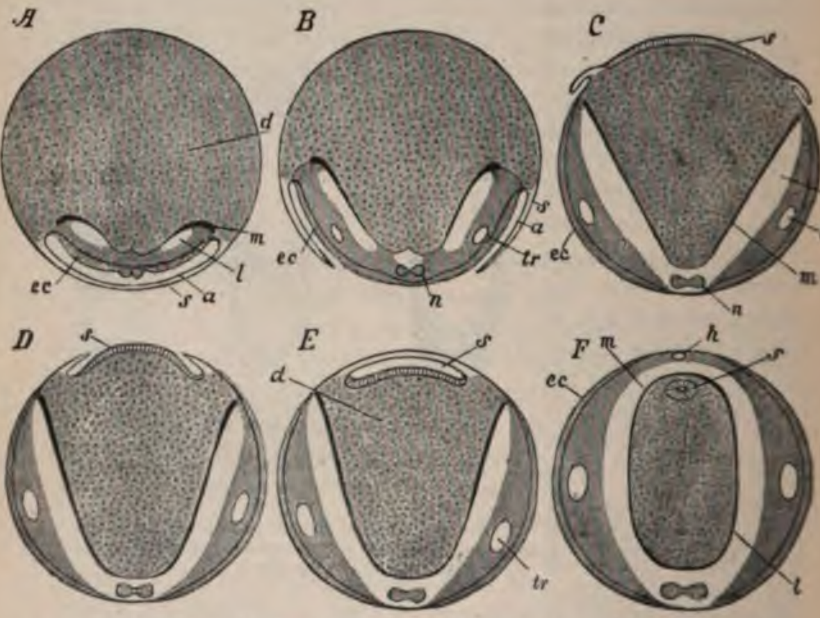

FIG. 150.—Diagrams illustrating the formation of the dorsal organ in *Hydrophilus* (after GRABER and KOWALEVSKY, from LANG'S *Text-book*). *A*, transverse section through the egg, the germ-band being still covered by the amnion (*a*) and serosa (*s*). *B*, the fused amnion and the serosa are now ruptured and drawn back as two lateral folds. *C*, contraction of the serosa (*s*), which becomes the dorsal plate, leads to the dorsal displacement of these folds (Fig. 149 *A*). *D*, the contracted serosa is now partly covered by these folds, which are now bent round dorsally (Fig. 149 *B*). *E*, the dorsal tube is completed by the fusion of these folds (Fig. 149 *C*). *F*, the enteron has become completed dorsally and has enclosed the dorsal tube (*s*). *a*, amnion; *d*, food-yolk; *ec*, ectoderm; *h*, heart; *l*, body-cavity; *m*, rudiment of enteron; *n*, nervous system; *s*, serosa (in *C* and *D*=dorsal plate, in *E* and *F*=dorsal tube); *tr*, lateral tracheal trunk.

embryo. The dorsal tube develops in an altogether similar way in the Orthoptera. When the enteron at a later stage closes dorsally, the dorsal tube, together with all the food-yolk, is enclosed within it (Fig. 150 *F*). In *Hydrophilus*, the dorsal plate and the dorsal tube are distinguished by their great length (Fig. 149); they extend over the whole dorsal surface of the egg. The closing of the dorsal tube, brought about by the fusion of the amniotic folds over it, here takes place from behind forward, so that for some time a pore is found anteriorly as the opening of the dorsal tube (Fig. 149 *C*).

B. Involution accompanied by dorsal withdrawal of the Amnion only.

This type has been observed in a few Coleoptera (*Chrysomelidae*, Fig. 151). The serosa (*s*) here remains entirely unaffected by the whole process of involution, and is retained till the late stages of development closely applied to the inner side of the chorion. The provisional enclosure of the yolk dorsally is brought about after the rupture of the ventral amnion by the dorsal growth (Fig. 151 *B*) of the latter (*am*). When, in later stages of development, the germ-band extends more and more over the dorsal surface of the egg (Fig, 151 *C*), the cells of the compressed amnion first accumulate dorsally (this accumulation has been described by **Wheeler** in *Doryphora* as the amniotic dorsal organ), and then break away from the aggregate and become scattered in the food-yolk, where they finally disintegrate (**Wheeler**, No. 95). To this type belong *Doryphora* (**Wheeler**), *Lina* (**Graber**), and perhaps also *Donacia* (**Melnikoff**, No. 53).

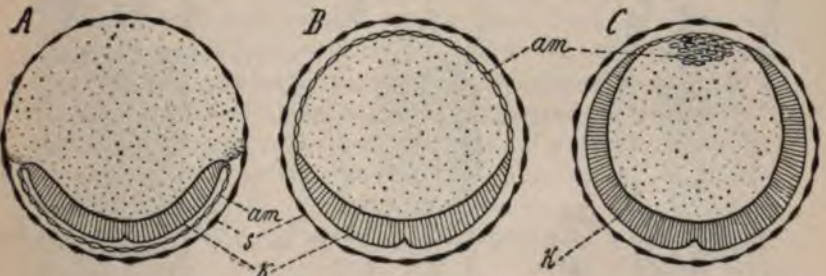

Fig. 151.—Diagrammatic transverse sections illustrating the formation of the dorsal body-wall in *Doryphora* (after Wheeler). *am*, amnion (in *B*, serving as the provisional dorsal integument; in *C*, undergoing disintegration); *k*, germ-band; *s*, serosa.

C. Involution accompanied by dorsal withdrawal of the Serosa and complete separation of the Amnion.

This type is closely related to the first. It was observed by **Graber** in *Chironomus* (Fig. 152) and the *Phryganeidae*. Here only the serosa (*s*) tears ventrally and contracts dorsalwards (Fig. 152 *B*), where it forms a dorsal organ closely resembling that of the Orthoptera and Rhyncota, which finally degenerates and sinks into the yolk (Fig. 152 *C*). The amnion at first remains unchanged. The completion of the dorsal region is brought about by the continuous approximation of the points of union between the amnion and the ectoderm; this produces a narrowing of the dorsal umbilical passage, which finally becomes obliterated by the fusion of its walls. The amnion then separates from the ectoderm, and up to the time of hatching surrounds the embryo as a closed sac (Fig. 152 *C*).

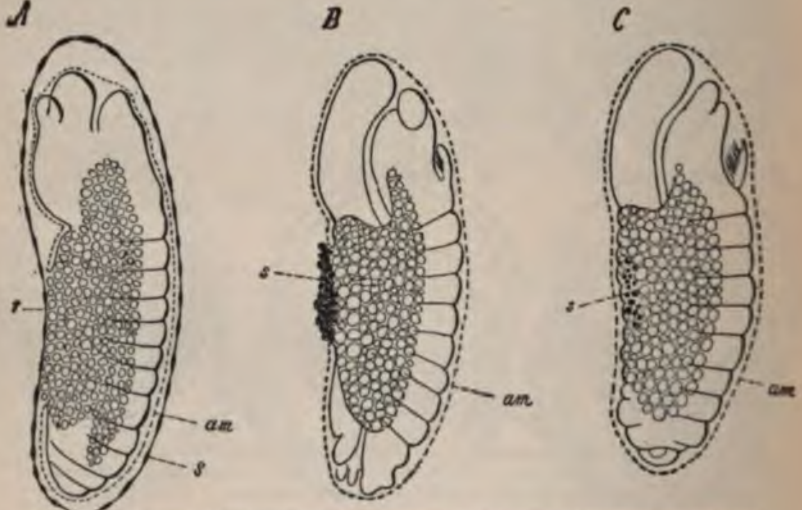

FIG. 152.—Involution of the embryonic integuments in *Chironomus* (diagram after GRABER). *am*, amnion; *r*, dorsal umbilicus; *s*, serosa, which in *B* has retracted dorsally and in *C* has been absorbed into the yolk.

D. Involution accompanied by the amputation of both Embryonic Envelopes.

This type may be derived from the preceding type if we imagine that the serosa is not ruptured nor in any way essentially modified. The dorsal extension of the germ-band, carrying with it the points of origin of the amniotic folds, causes a constriction of the dorsal umbilical passage and, by the fusion of its margins, completes the dorsal integument; the two membranes are first connected by a solid umbilical cord with the embryo and, when this breaks down, they become separated from the embryo and from one another (Fig. 143 *B*, p. 286). As two completely closed sacs, one within the other, they envelop the embryo, as has already been mentioned in the case of *Hylotoma*, up to the time of hatching. This type occurs in the Hymenoptera and the Lepidoptera. In the latter (Fig. 142 *C*, p. 285), in which the germ-band is immersed, remains of food-yolk are retained between the amnion and serosa, which, together with the large cells of the serosa, serve as the first nourishment for the young caterpillar (GANIN, No. 23).

E. General Considerations.

We must regard as the most primitive the first of these types of development, in which, after rotation of the germ-band and the development of a continuous amnion-serosa-sac, conditions are brought about resembling those usually found in the other Arthropoda, the serosa being invaginated and gradually degenerating. This is confirmed by the fact that this type is frequent in those orders of Insects which are generally claimed as the more primitive. The fourth type of development, on the other hand, in which the embryonic envelopes lose their continuity with the embryo and form two free membranes enclosing the latter, must be regarded as the most specialised. The third type is intermediate between these two. With regard to the way in which the serosa degenerates, it approaches the first type, but in the separation of the amnion resembles the fourth. The second seems to represent a type of formation of the dorsal integument independently acquired among the Coleoptera.

In the first type, the development of the amnion-serosa-sac is introduced by the rupture of the two fused embryonic envelopes. This rupture in the ventral median line in the *Libellulidae* takes place only in the cephalic region. In the second type only the serosa is affected by the rent, while, in the fourth type, both embryonic envelopes remain intact up to the time of hatching.

6. The formation of the Germ-layers.

The older accounts of the formation of the layers in the germ-band of the Insecta were very incomplete. BÜTSCHLI (No. 11) first found that, in *Apis*, a lower or inner layer is produced in the germ-band by an infolding. Soon after, KOWALEVSKY's researches (No. 48), carried out by means of sections, laid the foundation for more accurate knowledge. KOWALEVSKY found that, in *Hydrophilus*, a furrow appears running along the whole length of the rudiment of the germ-band (Fig. 134 *A*, *B*, *r*, p. 270), which, sinking in, yields the *lower or inner layer* of the germ-band, *i.e.*, the common rudiment of the entoderm and the mesoderm (Fig. 158 *A–C*, p. 321). A similar condition was found by KOWALEVSKY in *Apis*, in the Lepidoptera, and in a few other forms. This furrow must be regarded as the blastopore of an unusually long gastrula-depression, extending along the whole ventral surface as far as the point at which, later, the proctodaeum develops, and the edges of the furrow must be regarded as the lip of an exceedingly long blastopore. The tube which has arisen in *Hydrophilus* by the closing of this furrow may be claimed as the archenteron.

The first rudiments of the gastrula-furrow are, in the Insecta, yielded by two folds running longitudinally in the thickened ventral plate one on either side of the median line (Fig. 154, *f*, p. 313). These folds cut off a middle region of the ventral plate, the so-called *middle plate* (*m*) from the lateral plates (*s*). As the middle plate bends in and becomes grown over by the lateral folds, which mark the edges of the blastopore, the gastrula-depression is formed (Fig. 158 *A*, *r*, p. 321), the development of which causes the middle plate to become the lower or inner layer of the germ-band. The ectoderm of the germ-band is then derived from the lateral plates. The fusion of the edges of the blastopore, through which the closing of the archenteric tube is brought about, occurs latest in its most anterior region, at a part of the germ-band corresponding to that at which later the stomodaeal invagination develops.

In *Hydrophilus*, the gastrula-furrow develops in a way differing somewhat from that which usually prevails, as the middle part of the furrow here appears somewhat retarded in its development, while, in the anterior and posterior regions, the lips approximate earlier. This growth affects the outline of the blastopore, which at a certain stage is flask-shaped (Fig. 134 *A*, p. 270), the bulging of the flask corresponding to the part of the germ-band which is retarded in its development.

During the invagination of the middle plate and its transformation into the archenteric tube it becomes modified histologically (Fig. 158 *A* and *B*, p. 321). Whereas it primarily consisted of a columnar epithelium, which in the further course of development becomes multilaminar, the individual cells, pressed together, being wedge-shaped, the cells in later stages become more and more cubical or irregularly polygonal (Fig. 158 *B*), and also show a less regular arrangement. At the same time the archenteric tube becomes compressed dorso-ventrally. While it thus broadens out laterally under the lateral plates, its originally circular lumen passes into a horizontal slit, which in *Hydrophilus* long remains recognisable as the boundary between the two parts of the lower layer (HEIDER, No. 38).

A gastrula-furrow of this nature has been found in a great variety of Insecta by most of the recent workers on this subject. It must therefore be regarded as occurring universally. The fact that it was missed by Korotneff (No. 47) in *Gryllotalpa* is of no great importance. In the same way, the negative result obtained by Witlaczil (No. 98) in the *Aphidae* is hardly to be accepted when we consider Graber's account (No. 24) of the development of *Pyrrhocoris* and the recent researches by Will (No. 97) on the *Aphidae*, in both of which we find a gastrula-furrow described.

Many variations in detail are found in the process of gastrulation in the Insecta. It is not always accompanied by the development of such a distinct tube as that found in *Hydrophilus*. The invagination appears in individual cases to be less distinct and variously modified, so that three different types may here be established.

1. There is **actual invagination, accompanied by the formation of a tube** (Fig. 158 *A*, p. 321). The central region of the ventral plate (the middle plate) becomes invaginated, its lateral margins standing up as a couple of folds, each composed of a double layer of cells. These folds now grow towards the middle line and unite, thus forming a tube (*Hydrophilus*, *Musca*, *Pyrrhocoris*, etc.). Finally the cells of this tube lose their epithelial continuity and, becoming slightly separated, assume an irregular polygonal shape.

2. The middle plate may be **overgrown by free ectoderm-folds** (Fig. 153). The middle plate does not separate from the ectoderm of the germ-band through the union of folds as in 1 but, at the place where the lateral folds arise in other cases, the connection between the ectoderm and the middle plate becomes broken, and the free edges of the ectoderm grow over the sunken middle plate towards the middle line. Here also the cells of the middle plate only lose their epithelial continuity later. This type occurs in various Hymenoptera and Lepidoptera. It has been observed in *Apis* by Kowalevsky and Grassi (No. 32), and in Lepidoptera by Kowalevsky (No. 48), whose statements were confirmed by Bobretzky (No. 6).

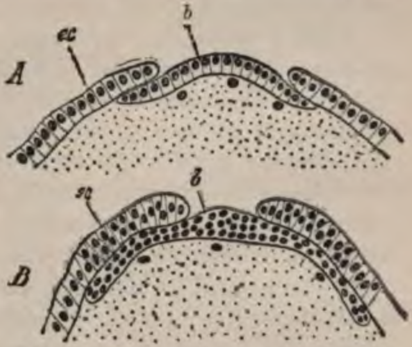

Fig. 153.—Transverse sections through the germ-band of *Apis* in two consecutive stages of gastrulation (after Grassi). *b*, lower layer; *ec*, ectoderm.

3. The lower layer may originate by **ingrowth of cells from a median groove.** The cells of the future lower layer here lose their epitheloid nature at an early period. A median groove is formed as in the other types, but there is no separation of a distinct median plate or tube, single cell-elements separate from the base of the groove and shift below the ectoderm; this proliferation of cells goes on until the lower layer is complete, its cells wandering below the ectoderm and the lateral parts of the germ-band. This type appears to occur in the *Aphidae*, according to Will (No. 97), and in the *Phryganeidae*, according to Patten (No. 65).

In the second and third types of formation of the lower layer, a tube with a distinct lumen naturally does not develop. The cell-mass of the lower layer is here, from its origin onwards, solid and gradually widens out below the lateral plates. The types given are connected by transitionary forms. Thus it appears, according to GRABER's recent statements (No. 30), as if, in the Lepidoptera, a type intermediate between the second and third types is occasionally to be observed.

It was observed by WHEELER in *Doryphora*, and by GRABER in *Lina*, that the most posterior end of the gastrula-furrow in certain stages appears forked (Fig. 145, p. 291), a condition which we are not in a position to explain.

The cell-layer derived from the gastrula-invagination (the lower layer) represents the common rudiment of the entoderm and the mesoderm. It has only recently become known in what way these two germ-layers are separated from one another in the Insecta. With regard to this point we must follow chiefly the statements of KOWALEVSKY as to the *Muscidae* (No. 49), of HEIDER as to *Hydrophilus* (No. 38), and WHEELER as to *Doryphora* (No. 95). KOWALEVSKY showed first in connection with *Musca* that the greater part of the lower layer yields mesoderm exclusively, and that only two cell-masses, corresponding respectively to the anterior and the posterior end of the germ-band, are concerned in the formation of entoderm. We must therefore, in the Insecta, speak of an anterior and a posterior entoderm-rudiment. As the stomodaeal and proctodaeal depressions which appear as ectodermal invaginations develop, the cell-masses of the two entoderm-rudiments are pushed in front of them into the interior, and thus become separated from the mesoderm. The two entoderm-rudiments now represent cell-accumulations closely applied to the blind ends of the stomodaeum and proctodaeum. They soon broaden out into the shape of watch-glasses, with their concavities directed towards each other and their convex sides turned to the respective poles of the egg. Their shape, however, soon changes, two lateral bands growing out from each rudiment in such a way as to form the letter U (Fig. 154, *en*). The ends of the two U-shaped rudiments are directed towards each other, and grow out until they meet and fuse. The entoderm-rudiment yielded by the fusion of the two U-shaped rudiments then consists of two bands running longitudinally above the germ-band, mostly dorsal to the primitive segments. Anteriorly and posteriorly these bands pass into one another, and at these points fuse closely with the stomodaeal and proctodaeal invaginations. As these lateral entoderm-bands gradually widen, they begin to grow round the surface of the food-yolk on which they lie. This circumcrescence as a rule progresses most rapidly on the ventral side, so that the two entoderm-bands unite first in the ventral middle line and only later in the dorsal middle line. The food-yolk in this way comes to lie entirely within the rudiment of the enteron (p. 336).

In the *Muscidae* (and in a few other forms) the whole of the food-yolk is not taken into the enteron, but a small amount remains in the body-cavity anteriorly and posteriorly, and is there absorbed.

Kowalevsky has already pointed out that it is only the median portions of the lower layer which are separated as entodermal rudiments at the anterior and posterior ends of the germ-band by the ingrowth of the stomodaeum and proctodaeum. The lateral parts in these regions give rise to mesoderm. Kowalevsky has therefore compared the formation of the germ-bands in the Insecta with their formation in *Sagitta*. This view has received thorough support from more recent researches made on Coleoptera (Heider, No. 38; Wheeler, No. 95). Even before the stomodaeal and proctodaeal invaginations appear, the entoderm-rudiments can here be seen rising as a median growth from the base of the gastrula-furrow (Fig. 155), while the lateral mesodermal parts appear in the form of lateral sacs (Fig. 154 *B* and *D*). The separation of the germ-layers in the Insecta thus resembles somewhat the condition observed in *Sagitta*, where the archenteron becomes divided by the appearance of two folds into a median enteric rudiment and two lateral coelomic sacs (Vol. i., p. 368). The chief peculiarity in the Insecta arises

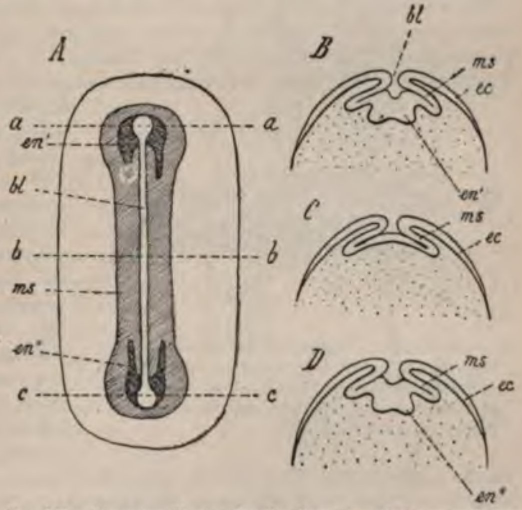

Fig. 154.—Diagrams illustrating the formation of the germ-layers in *Doryphora* (after Wheeler). *A*, surface view. *B*, transverse section through the anterior end of the germ-band at the level of the line *aa*. *C*, transverse section through the middle of the germ-band corresponding to the line *bb*. *D*, transverse section through the posterior end of the germ-band corresponding to the line *cc*. *bl*, blastopore; *ec*, ectoderm; *en'*, anterior U-shaped entoderm-rudiment; *en''*, posterior U-shaped entoderm-rudiment; *ms*, mesoderm.

from the great lengthening of the gastrula-invagination. We may assume with **Rabl*** for the median invaginating plate a median unpaired entoderm-band and paired mesoderm-bands. The entoderm-band is, however, dragged apart to form an anterior and a posterior portion by the great lengthening of the furrow (Fig. 154, *en′*, *en″*), so that over the greater part of the germ-band the two lateral mesoderm-bands meet one another in the median line.

The view just mentioned would receive important support from the statement of **Bütschli** (No. 12) that, in the formation of the germ-layers at the posterior end of the germ-band of *Musca*, the archenteron actually becomes divided up at a certain stage through the formation of folds into three connected diverticula: of these diverticula, the unpaired median one is to be regarded, just as in *Sagitta*, as the entoderm-rudiment and the paired lateral ones as the mesoderm-rudiment (coelomic sacs). Since, however, the more recent works on the ontogeny of *Musca* do not confirm this statement, and the conditions described may, as we shall see, perhaps be interpreted in another sense, we must leave this point for the present undecided.

The statements made by **Kowalevsky** (No. 49) with regard to the formation of the germ-layers in *Musca* have been only partially confirmed by the later researches of **Voeltzkow** (No. 85) and **Graber** (No. 28) on the same animal. According to **Voeltzkow**, the stomodaeal and proctodaeal invaginations grow inwards from the base of the gastrula-furrow, and therefore belong, not to the ectoderm, but to the lower layer. The anterior and posterior entoderm-rudiments are said to arise by the proliferation of cells from the blind ends of these two invaginations. **Graber** (No. 28), indeed, has confirmed **Kowalevsky's** statements for the anterior entoderm-rudiment, and also assumes the ectodermal origin for the stomodaeum. As to the proctodaeum, on the contrary, and the posterior entoderm-rudiment, **Graber** entirely agrees with **Voeltzkow**, with the single exception that, for the growth of the posterior entoderm-rudiment, he claims not only the blind end, but a long band of the ventral side of the proctodaeum. We may here object to this view of **Voeltzkow** and **Graber** that if, in reality, in the *Muscidae*, a posterior section of the intestine arose by invagination from the lower layer, we should not be able to call it the proctodaeum, for in that case we should not be able to regard it as homologous with the similarly-named section of the intestine of other Insects, in which it forms, as in all other animals, from the ectoderm. It, however, appears to us that the sections of the posterior end of the germ-band of the *Muscidae*, which are in any case difficult to understand, can be more

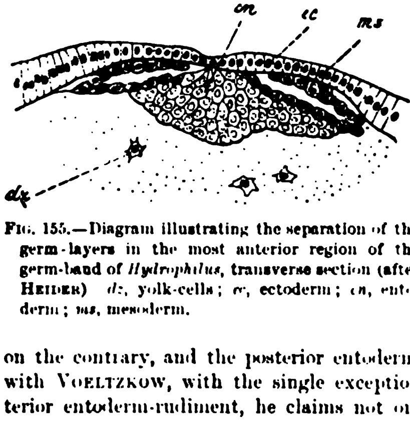

Fig. 155.—Diagram illustrating the separation of the germ-layers in the most anterior region of the germ-band of *Hydrophilus*, transverse section (after **Heider**) *dz*, yolk-cells; *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm.

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* Theorie des Mesoderms. *Morph. Jahrb.* 1889.

satisfactorily explained by interpreting the parts differently, as GRABER formerly did (No. 27). We may perhaps assume that, in the *Muscidae*, as in *Chironomus*, the posterior end of the germ-band not only sinks into the yolk, but also makes a hook-like bend inwards, so that the germ-band in transverse sections of this region is cut through three times. In this way, the posterior end of the germ-band, sunk into the yolk, and the part lying in reality anterior to it, but in transverse section appearing on the dorsal side of the egg, are, by means of the still open gastrula-groove, in communication in such a way that, in a series of transverse sections, the lumina of portions of the gastrula-furrow belonging to these two parts flow together, thus yielding the peculiar dumb-bell-shaped figure. By this assumption, the invagination which VOELTZKOW and GRABER (No. 28) erroneously held to be the proctodaeum would more correctly appear as the so-called germ-prominence (p. 276), and the lumen of this invagination would then have to be considered as the amniotic cavity, and the aperture at its dorsal side, not as the anus, but as the aperture of that cavity. The proctodaeum seems to appear only later in the form of an invagination from this cavity. This view is supported throughout by RITTER's observations of the development of the proctodaeum (No. 71).

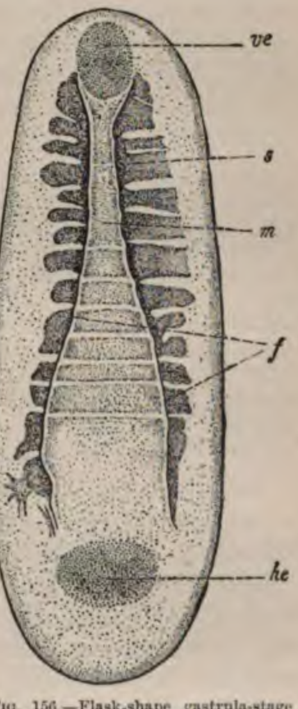

FIG. 156.—Flask-shape gastrula-stage of *Chalicodoma* (after CARRIÈRE). *f*, folds which bound the middle plate laterally (lips of the blastopore); *m*, the partly segmented middle plate (here mesoderm-rudiment); *s*, the segmented lateral plates (later ectoderm of the germ-band); *ve*, anterior entoderm-rudiment; *he*, posterior entoderm-rudiment.

We must here mention GRABER's view of the presence of a lateral gastrulation in the *Muscidae*. GRABER finds, in the germ-band of the *Muscidae*, near the median or principal gastrula-furrow, lateral folds which are specially marked in the most anterior and posterior parts of the germ-band, and which are said to give off elements to the lower layer. These paired folds, which were already known to BÜTSCHLI (No. 12) and VOELTZKOW (No. 85), and which mark the lateral edges of the germ-band, are, according to GRABER, supplementary gastrula-furrows which serve the purpose of supporting the gastrula-furrow in its plastic activity in the formation of the lower layer. GRABER has, however, not proved that elements are given off from these lateral folds to the lower layer. Since it was already known to VOELTZKOW that, in the stage under consideration, the portion of the blastoderm not taking part in the formation of the germ-band shows a great tendency to the formation of folds, these folds probably come under this category, and ought not to be regarded as connected with the further development of the embryo.

The formation of the germ-layers in the Hymenoptera seems to deviate somewhat from the common type. KOWALEVSKY and GRASSI (No. 32),* indeed, agree that here also the entoderm originally forms a part of the lower layer. But the separation of the entoderm from the mesoderm in *Apis* takes place in such a way that the two ends of the lower layer bend over the dorsal side of the egg, and the anterior and posterior entoderm-rudiments which have thus come to lie on the dorsal side grow towards one another. When the two rudiments, which here also are horseshoe-shaped, have met and fused, the circumcrescence of the food-yolk begins; in this case the process thus starts from the dorsal side and is completed on the ventral side. It results from this that the layer of entoderm-cells in *Apis* at first does not lie below the germ-band, but on the dorsal side of the egg below that flattened epithelium which, arising from the amniotic fold, provisionally completes the dorsal surface (p. 287).

The condition of the entoderm-rudiment in *Chalicodoma* is somewhat similar (CARRIÈRE, No. 13). Here also the entoderm-bands do not lie below the germ-band, but extend beyond the latter towards the dorsal side of the egg. As to the first separation of the germ-bands, CARRIÈRE arrived at views approaching those just described, but still revealing in the case of *Chalicodoma* a peculiar type. The middle plate (*m*), which becomes invaginated by the formation of the gastrula-furrow, and which, like the lateral plates, shows signs of segmentation at an early stage, is here said to yield the mesoderm exclusively, while the anterior and posterior entoderm-rudiments (*ve* and *he*) arise from a growing zone closely succeeding the middle plate, in the region of which the separation of the mass of entoderm-cells by delamination from the superficial cell-layer which remains in continuity with the ectoderm takes place.

We have still to mention the *yolk-cells* and the *secondary cleavage of the yolk*. The yolk-cells are elements scattered in the food-yolk, some being cells which remained in the yolk at the time when the blastoderm formed (Fig. 131 *C* and *D*, *z*, p. 265), and some having reached the yolk by subsequent immigration from the blastoderm and its derivatives. GRABER first pointed out the immigration of cells from the lower layer into the yolk, and his observations have been confirmed by other authors. In individual cases, indeed (*e.g.*,

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* GRASSI's researches mark a turning-point in the conception of the formation of the germ-layers in the Insecta. It must be recorded to his credit that he was the first to oppose the universal opinion of the time that the yolk-cells represented the actual entoderm of the Insecta, and to prove that the entoderm is a part of the lower layer. The presence of an anterior and a posterior entoderm-rudiment was also correctly made out by him. His views were adopted only later by KOWALEVSKY (No. 49) and HEIDER (No. 37), though it should be pointed out that the views put forward by KOWALEVSKY in his first treatise nearly coincided with what is now known to be the actual condition.

in *Melolontha*), these later immigrated cells are said to be clearly distinguishable by their histological character from the cells originally found in the yolk.

The yolk-cells are distributed in a regular manner through the food-yolk. Their principal function appears to be digestive, particles of food-yolk being taken up by these cells and changed in such a way as to render the yolk assimilable by the growing cells of the embryo. This leads, after the development of the germ-band is completed, to the marking-off of the territories belonging to the individual yolk-cells, and this process has been described as *secondary yolk-cleavage* (Fig. 158 *C–F*, p. 321; Fig. 135, p. 273). In individual cases (*Apis, Musca*) such cleavage, however, seems not to occur. The yolk-cells can still be recognised in the completely developed enteron in the remains of food-yolk which fill it, and here they gradually disintegrate.

It was long considered by followers of DOHRN, BALFOUR, and HERTWIG that the yolk-cells represented the actual entoderm of the Insecta, as it was thought that these cells finally became arranged at the surface of the food-yolk to form the enteric epithelium. This view has to be relinquished in face of the more recent researches, on which the account of the formation of the germ-layers given above is founded. It appears that the yolk-cells do not in any way take part in the formation of the embryo. It was indeed suggested in several quarters that they gave rise finally to blood-corpuscles or parts of the fat-body (DOHRN, No. 21, TICHOMIROFF, No. 79, and especially WILL, No. 97). A number of more recent authors, however, oppose this view, and maintain that the yolk-cells, after having fulfilled their function as vitellophags, simply disintegrate. This last view seems to us the most probable, since another origin has been proved for the fat-body and the blood-corpuscles (p. 341).

Bearing in mind the statements made above in connection with the Crustacea (Vol. ii., p. 144), we may probably regard the yolk-cells as an abortive portion of the entoderm.

[Recent observations have once more rendered uncertain the origin of the mesoderm, the nature of the epithelium lining the alimentary canal, and the true significance of the primitive groove. Thus HEYMONS (Nos. XV. and XX.), states that in the Orthoptera, the ento-mesoderm of other authors is to be regarded as consisting of mesoderm only, the lining of the definitive alimentary canal arising from the ectodermal epithelium of the stomodaeum and proctodaeum. He further states that the primitive groove (blastopore of authors) may be completely wanting, and even when present is not to be regarded as connected with gastrulation. LÉCAILLON (No. XXIX.) finds that in the *Chrysomelidae* the whole alimentary canal is ectodermal. These two authors think that the higher Insects exhibit no entoderm in the alimentary canal of the adult, while in the lower forms (HEYMONS, No. XVI., *Lepisma*) the enteron arises from the yolk-cells. On the other hand, BÜRGER and CARRIÈRE (No. II.), with whom WHEELER agrees, are fully convinced that a true enteron exists in *Chalicodoma*, and entirely dissent from HEYMONS' views. They show that the entoderm arises from the undifferentiated blastoderm, and that the stomodaeal and proctodaeal invaginations arise from the superficial layer of blastoderm-cells, the only layer that can properly be called ectoderm. See also HEIDER (No. X.).—ED.]

7. Further development of the Mesoderm.
Development of the Body-cavity.

We have seen (p. 271) that an invagination running along the whole length of the germ-band gives rise to a layer of cells, which soon extends on the inner side of the germ-band and so forms a second, lower layer (Fig. 158 *C*). From this layer, at the anterior and posterior extremities of the germ-band, the entoderm becomes separated and becomes closely applied to the stomodaeal and proctodaeal invaginations which have meantime arisen. The remaining and by far the largest part of the lower layer may, from this stage onward, be considered as *mesoderm*.

An arrangement of the latter into two lateral bands (mesoderm-bands) now takes place, its cells withdrawing more and more from the median line (Fig. 158). This withdrawal from the median line is, however, not complete. Into the space between the two mesoderm-bands the yolk often thrusts itself, giving rise to the so-called *median ridge*. Segmental cavities (*cavities of the primitive segments, us*) now appear in the lateral parts of the mesoderm, and the mesoderm-cells become arranged as an epithelium round these cavities and form the wall of the *primitive segments* or *coelom-sacs*.

The cavities of the primitive segments arise, as a rule, by a splitting of the mesoderm. HEIDER (No. 38) thought that in the case of *Hydrophilus* he had convinced himself that they arose merely by the widening of a slit, which was already recognisable at an earlier stage between the two layers of the mesoderm, and which could be traced back to the lumen of the archenteron compressed dorso-ventrally. GRABER (No. 30), however, in his more recent investigations on this point, was not able to satisfy himself of the persistence of these slits. On the other hand, HEIDER'S view has been confirmed by CARRIÈRE (No. 13) in the case of *Chalicodoma*. These observations afford support to the view first adopted by O. and R. HERTWIG that the cavities of the primitive segments in the Insecta represent paired diverticula of the archenteron.

The large primitive segments of *Phyllodromia* arise in a different manner from those of *Hydrophilus*. The mesoderm of the germ-band is here at first only a single layer of cells. This simple layer, as the limb-rudiments develop, separates with the ectoderm from the surface of the food-yolk, and cavities thus arise in every segment, these cavities, surrounded by mesoderm-elements, becoming the closed coelomic sacs (HEYMONS, No. 43).

The parts of the mesoderm lying laterally in the germ-band are used in the formation of the primitive segments (Fig. 158 *D* and *E*). Not all the mesodermal elements, however, enter into their formation. Some of the mesoderm-cells which lie nearer the median line always remain distinct (*cf.* Fig. 157 *A*, *m*). The greater the size of the primitive segments, the smaller is this remainder. and *vice versâ*. These elements are irregularly arranged and represent a kind of mesenchyme.

It was pointed out by HEIDER (No. 38), and recently by GRABER (No. 30),

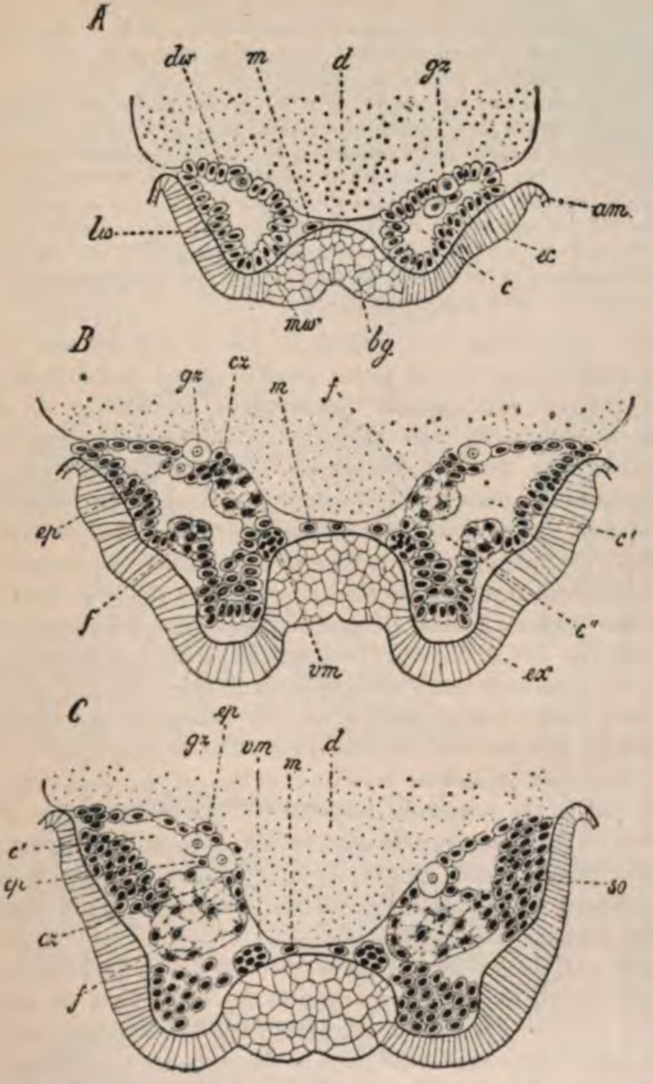

Fig. 157.—Transverse sections through the abdominal region of three consecutive stages in development of *Phyllodromia germanica* (after Heymons). *am*, amnion; *bg*, rudiment of the ventral chain of ganglia; *c*, coelomic cavity; *c'*, dorsal, and *c''*, ventral portion of the coelomic cavity; *cz*, cells of the primitive segments which become applied to the genital rudiment; *d*, food-yolk; *dw*, dorsal wall of the coelomic sac; *ec*, ectoderm; *ep*, epithelial cells; *ex*, abdominal limb-rudiments; *f*, rudiment of the fat-body; *gz*, genital cells; *lw*, lateral wall of the coelomic sac; *m*, mesoderm-cells which do not take part in the formation of the coelomic sacs; *mw*, median wall of the coelomic sac; *so*, somatic mesoderm-layer; *vm*, ventral longitudinal muscle.

that the boundaries of the consecutive primitive segments which are marked by dissepiments do not always exactly coincide with those of the segments of the germ-band. This is especially noticeable in later stages, and is caused by the former shifting a little in position.

As a rule, each true segment of the primary trunk has a pair of primitive segments. Besides these, a pair of coelomic sacs develops in the primary cephalic region in *Blatta* (CHOLODKOWSKY, No. 19), in *Stenobothrus* and *Mantis* (GRABER, No. 30). These sacs would correspond to the cephalic cavities in *Peripatus* (p. 199). The Orthoptera also appear to have a pair of coelomic sacs in the terminal segment (CHOLODKOWSKY). In *Hydrophilus*, on the contrary, the coelomic sacs are not only wanting in the cephalic and anal regions, but appear suppressed in the mandibular segment, and their development is delayed in the first maxillary segment (HEIDER).

The coelomic sacs vary greatly in size in the different groups of Insects. They develop to the greatest extent in the Orthoptera (Fig. 157), in which almost the whole cell-material of the mesoderm is used up in their formation, and in which, according to CHOLODKOWSKY (No. 19), GRABER (No. 30), and HEYMONS (No. 43), the conditions under which the coelom develops bear considerable resemblance to those described in connection with *Peripatus* (p. 199 *et seq.*). The very extensive cavities of the primitive segments which, in the Orthoptera, reach into the limb-rudiments also (Fig. 157 *B*, *ex*), at a later stage are broken up by constrictions into dorsal and ventral halves (Fig. 157 *B*, *c'*, *c''*). The ventral halves (*c'*), which extend into the limb-rudiments, soon degenerate (Fig. 157 *C*), the cells of their walls losing their epithelial continuity and becoming irregularly grouped like a mesenchyme. The shifting apart of these cells and their separation from the surface of the food-yolk then gives rise to the *permanent body-cavity*. The dorsal halves of the cavities of the primitive segments, on the contrary, are long retained (as will be seen below, p. 338) and play an important part in the development of the layer of intestinal fibres, the heart, the pericardial septum, and the genital organs.

In the higher groups of Insecta (the Coleoptera, Lepidoptera, and Hymenoptera), the primitive segments no longer form on such an extensive scale (Fig. 158 *D–F*, *us*). They are here comparatively small sacs lying in the lateral parts of the germ-band, and correspond to the dorsal parts only of the coelomic sacs of the Orthoptera. The ventral parts are here from the very first replaced by mesenchyme. There are consequently, in these forms, no coelomic diverticula in the limb-rudiments.

In the *Muscidae*, the development of coelomic sacs is apparently completely suppressed (GRABER, No. 28). We find their equivalent here in diverticula,

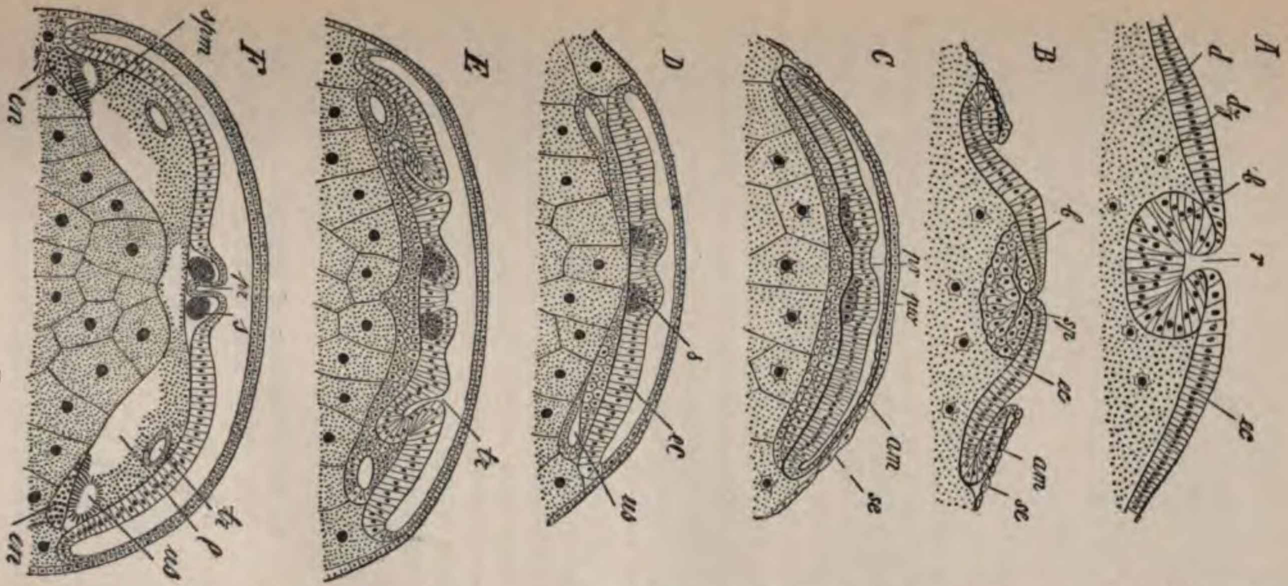

FIG. 158.—Transverse sections through the germ-band of *Hydrophilus* at six consecutive stages (after HEIDER, from LANG'S *Text-book*). *A*, gastrula-stage (Fig. 134 *A*, at the point *a*, p. 270). *B*, transverse section through the stage *D*, Fig. 134, at the most anterior part of the germ-band, where it is not yet completely grown over by the amniotic fold. *C*, transverse section through a trunk-segment at the stage depicted in Fig. 134 *E*. *D*, *E*, *F*, sections through older stages. *am*, amnion; *b*, lower layer; *d*, food-yolk; *dz*, yolk-cells; *ec*, ectoderm; *en*, entoderm; *l*, future body-cavity; *pr*, primitive or neural groove; *pw*, primitive swelling of the ventral ganglionic chain; *r*, blastopore; *sp*, slit in the mesoderm (remains of the lumen of the archenteron); *se*, serosa; *s*, lateral strand of the rudiment of the ventral ganglionic chain; *spm*, splanchnic layer of the mesoderm; *tr*, rudiment of a trachea (in *E*, as an invagination of the ectoderm; in *F*, in transverse section); *us*, primitive segment (= coelomic sac).

which appear at a comparatively late stage and run out from the definitive body-cavity.

The mesoderm-bands, which become separated, unite again later, the mesenchyme-cells from the one side becoming closely applied to those from the other in the median line. After the median yolk-ridge degenerates, a cell-accumulation often forms here (Fig. 158 *E*); this extends below the rudiment of the ventral chain of ganglia and owes its origin to the mesenchyme-cells. It is this cell-strand which has been called by NUSBAUM (No. 57) the chorda of the Insecta. It is finally used up in the formation of connective and other mesodermal tissues.

The *permanent body-cavity* of the Insecta arises quite independently of the coelomic cavities, by a separation of the germ-band from the yolk (BÜTSCHLI, No. 11, Fig. 158 *F, l*). It appears to be bounded on the one hand by the surface of the food-yolk and on the other by the irregularly arranged mesenchyme-cells. We can at first distinguish in section three distinct subdivisions of the body-cavity (*Hydrophilus*, HEIDER): a median space and two large paired, lateral spaces which unite later with one another, and with other lacunae which have arisen by the shifting apart of the mesenchyme-cells (*e.g.*, in the limbs). We may trace back the spaces of the permanent body-cavity, as in *Peripatus* (p. 201), to the primary body-cavity or cleavage-cavity. It becomes apparent as a series of lacunae in the mesenchyme and everywhere shows the character of a pseudocoele (*cf.* Introduction, Vol. i., p. 11).

In later stages of embryonic development, the coelomic sacs and the permanent body-cavity enter into communication (Fig. 167 *A*, *us*, *lh*). The consecutive coelomic sacs first fuse together through the degeneration of the transverse dissepiments that separated them; a slit then opens in the median wall of the coelomic sacs and connects their lumina with the permanent body-cavity. In the later transformations undergone by the wall of the coelomic sacs, the latter can no longer be recognised as separate sections of the whole body-cavity.

8. The Formation of Organs.

A. Outer Integument.

The hypodermis arises by direct transformation from the cells of the ectoderm. In later embryonic stages, the cuticle of the youngest larval stage is secreted at the surface of the hypodermis. The accessory structures, such as hairs, setae, etc., rise from specially large hypodermal cells (*setal mother-cells*, TICHOMIROFF, No. 78). Similar cells (*scale mother-cells*) give rise in the pupae of the Lepidoptera to the scales of the wings (SEMPER, No. 126).

B. Endo-skeleton.

The endo-skeleton of the head (*tentorium*) develops out of two pairs of ectodermal invaginations; the anterior invagination develops on the inner side of and somewhat in front of the mandible, the posterior within and somewhat in front of the second maxilla. The anterior pair becomes connected with the posterior and gives off two supporting columns which ascend on the inner surface of the clypeus towards the dorsal side. The median fusion of the posterior pair leads to the bridging over of the sub-oesophageal ganglion and, in many Insects, a transverse trabecula is thus formed in the cavity of the posterior part of the head (TICHOMIROFF, GRASSI, PATTEN, HEIDER, CARRIÈRE).

Similar ectodermal invaginations bring about the development of a chitinous tendon for the flexor mandibulae and a similar smaller tendon for the antagonistic muscle.

HATSCHEK (No. 36), who was unaware of the relation of these invaginations to the hard structures of the head, thought them to be tracheal invaginations. They have been regarded in the same way recently by CARRIÈRE (No. 13). Since this kind of endo-skeleton is found in other groups (*e.g.*, the Crustacea, Vol. ii., p. 160), and the hypothetical transformation of a trachea into an endo-skeletal structure of this kind involves the idea of a considerable change of function, we do not consider the homology between the invaginations under consideration and tracheal invaginations sufficiently well established. We are inclined to regard the former as structures of a distinct character, all the more so that they do not by any means everywhere agree so closely in position with tracheal stigmata of the following segments as they do in *Chalicodoma*.*

C. The Nervous System.

All the parts of the nervous system are derivatives of the ectoderm and appear in the embryo as ectodermal thickenings. The rudiment of the *ventral chain of ganglia* is found, as was first shown by HATSCHEK, soon after the gastrula-invagination closes, in the form of two longitudinal ectodermal thickenings running on either side of the median line. These are the so-called *primitive swellings* (Fig. 147 *A*, p. 297), which extend from the cephalic region to the terminal segment and show between them a median depression, the *primitive groove* (Fig. 158 *C*, *pr* and *pw*). Soon after the appearance of the primitive swellings, the first signs of segmentation can be seen on them, the swellings being thicker near the middle of the body-segments than at their boundaries. The primitive swellings pass anteriorly at the sides of the oesophageal

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* [*Cf.* footnote, p. 78.]

invagination (rudiment of the oesophageal commissures) on to the cephalic segment, and from the first are directly connected with the rudiment of the brain which develops from a thickening of the cephalic lobes. This character has recently been specially emphasised by Patten (No. 67), and has also been maintained by Heider (No. 38) and Graber (No. 30) against Will (No. 97), who considers that the brain-rudiment of the *Aphidae* (neural plate) arises independently and becomes connected with the rudiment of the ventral chain of ganglia through the oesophageal commissures which arise only secondarily as in the Crustacea (*cf.* Vol. ii., p. 160, footnote).

The widenings of the primitive swellings in the segments give rise to the ganglia of the ventral chain, and the inter-segmental constrictions to the paired longitudinal commissures.

Transverse sections (Fig. 158 *C*, p. 321, and Fig. 135, p. 273) show that the ectoderm becomes multilaminar in the region of the primitive swellings (*pw*). At a later stage, the lower layers separate by delamination from the superficial layers (Fig. 158 *D–F*, *s*) and form the so-called *lateral cords*, *i.e.*, the rudiments of the longitudinal strands of the ventral chain of ganglia. The primitive groove (*pr*) deepens meantime and forms an invagination extending between the lateral cords. The cells at the base of this invagination represent the so-called *middle cord* and give rise in the middle of the segments to the transverse nerve-commissures of the different pairs of ganglia (Hatschek).

With regard to the condition of the middle cord in the inter-ganglionic region, opinions are still divided. Hatschek's view that the primitive groove flattens out in this region, its wall being used up entirely for the formation of hypodermis, has been generally accepted, but Graber maintains (No. 30) that in this region also a median cord splits off which degenerates at a later stage.

The nerve-fibrillae arise first on the inner or basal surface of the lateral strands and the middle strand. Secondarily, by shifting their position, they become enveloped by ganglionic cells (*cf.* on a similar condition in the Crustacea, Vol. ii., pp. 160 and 161).

Leydig stated that, in many Insects, there is a double transverse commissure in each of the ganglia of the ventral cord, and a corresponding double rudiment has been repeatedly shown to exist in the embryo (Patten, No. 66; Ayers, No. 1; Heider, No. 38; Wheeler, No. 95; Graber, No. 30). No detailed accounts have as yet been given of the manner in which the nerves given off peripherally by the ganglia of the ventral cord arise.

The ventral diaphragm bridging over the ventral ganglionic chain (Fig. 167 *A*, *dv*, p. 340), which has been observed in many Insects, is derived by Korotneff (No. 47) from the mesoderm, but Heider (No. 38) believes that he was able, in *Hydrophilus*, to trace its origin back to ectoderm-cells lying laterally to the rudiments of the ganglia.

An unusually regular arrangement of the cells is shown in sections through the rudiments of the ventral cord in many Orthoptera (Fig. 159). **Wheeler** (No. 94) has recently recognised as "neuroblasts" four large cells (n–n) lying on each side on the surface of the lateral cords in *Xiphidium;* these cells, by repeated tangential division, give rise to the ganglionic cells, which are consequently arranged in vertical columns (z). **Graber** (No. 30) and **Viallanes** (No. 84) have observed similar phenomena, the former in *Stenobothrus* and the latter in *Mantis.** The middle cord, according to **Wheeler**, has neuroblasts (m) only in the interganglionic region; these, however, soon shift to the posterior side of the transverse commissures. In any case, as **Wheeler** has pointed out, the presence of eight longitudinal rows of neuroblasts points back to a similar condition in the Annelida, where only two such rows, produced from neuroblasts, are found (Vol. i., p. 294).

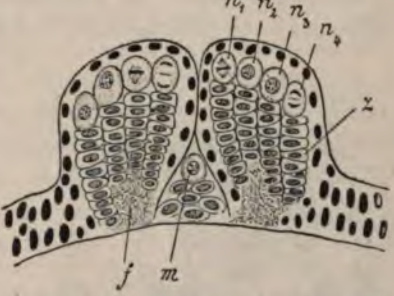

Fig. 159.—Transverse section through the rudiment of the ventral cord of *Xiphidium* (after **Wheeler**). f, fibrous tissue in transverse section; m, neuroblast-cells of the median cord; n_1–n_4, neuroblasts of the lateral cords; z, column of ganglion-cells proceeding from the neuroblasts.

The rudiments of one pair of ganglia of the ventral chain originally appear in each of the sixteen segments of the primary trunk. Fusion may occur between these rudiments later, and may bring about an apparent reduction in their number. The ganglia of the three maxillary segments, for instance, unite to form the sub-oesophageal ganglion, and the last pairs of abdominal ganglia fuse in varying numbers, shifting further forward at the same time. In individual cases (*e.g.*, many Diptera), a considerable concentration of the ventral cord is brought about by the fusion of consecutive pairs of ganglia.

The **brain (supra-oesophageal ganglion)** develops in the anterior region of the expanded cephalic lobes. We can, at an early stage, distinguish in the brain-rudiment the following sections:—

1. Paired thickenings of the ectoderm running forward at the

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* [**Bürger** (No. II.) finds that the ganglionic cells in *Chalicodoma* arise similarly from neuroblasts, but the arrangement is not so regular as that observed by **Wheeler** in *Xiphidium* and *Doryphora*.—Ed.]

sides of the oral aperture into the anterior cephalic region, which represent direct prolongations of the primitive swellings (Fig. 160, b^1, b^2, b^3), and from which are derived those parts of the brain known as the primary ganglia, and named by VIALLANES the *protocerebrum*, *deutocerebrum*, and *tritocerebrum*. These swellings become early separated as three consecutive brain-segments. PATTEN (No. 67) has the merit of having first drawn attention to this segmentation.

2. A large ectodermal thickening lying laterally to the swellings in the cephalic lobes just mentioned (Fig. 160 *A*, *og*). This is the rudiment of the *optic ganglion*, which exhibits in its postero-external

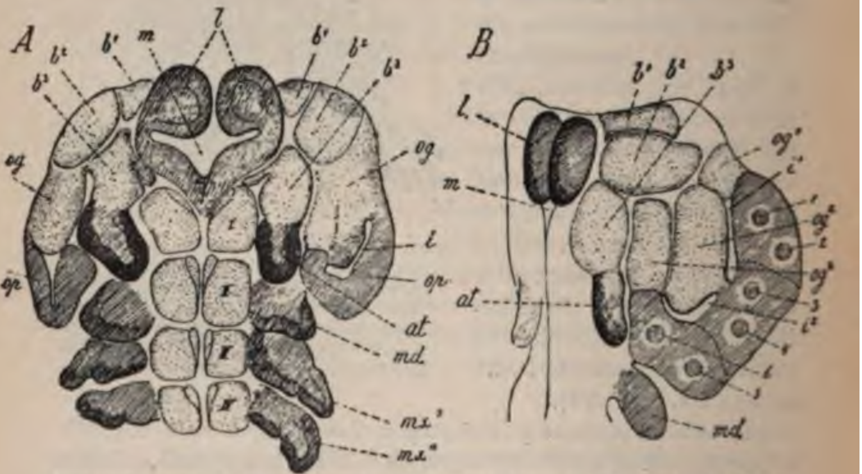

FIG. 160.—Diagram of the development of the brain in *Acilius* (after PATTEN). *A*, anterior end of the germ-band of an *Acilius* embryo. *B*, the same in three-quarter profile. *at*, antenna; b^1, first, b^2, second, b^3, third segments of the brain; *i*, invagination of the optic ganglion; i^1, anterior, i^2, posterior portions of the invagination; *l*, paired rudiment of the upper lip; *m*, mouth; *md*, mandible; *mx'*, first, *mx''*, second maxilla; *og*, optic ganglion; og^1, first, og^2, second, og^3, third segment of the optic ganglion; *op*, optic plate; *1–6*, rudiments of the six larval eyes; *I–IV*, the four anterior segments of the ventral chain of ganglia; *I*, that belonging to the pre-mandibular segment (?); *II*, that belonging to the mandibular segment; *III* and *IV*, those belonging to the first and second maxillae.

region a semi-circular ectodermal invagination (*i*, PATTEN's ganglionic invagination), which yields further elements for increasing the optic ganglion, and corresponds in position with a similar invagination found in the Decapoda (Vol. ii., p. 171) and the Arachnida (pp. 12 and 53).

The part of the ectoderm lying externally to this invagination (Fig. 160 *A*, *op*) also becomes thickened, increases considerably in extent, and yields at a later period a large part of the cephalic integument and the rudiments of the eyes; it is therefore known as the *optic plate*.

The separation of the brain-rudiment from the ectoderm, like that of the lateral cords, takes place by a process of delamination. An exception to this rule is found in the composition of the optic ganglion, which is formed from the invagination described above. The fibrous tissue of the brain develops here as in the lateral cords, first on the inner surface of the brain-rudiment, and only later sinks into the interior of the brain and becomes surrounded with a layer of ganglionic cells.

The rudiments of the two halves of the brain are originally distinct from one another. Later, when the dorsal part of the head has formed, the two halves of the brain shift on to the dorsal side, approaching one another until, finally, with the assistance of a median invagination (like the transverse commissures of the ganglia of the ventral cord), a commissural connection is established between them (GRASSI, No. 32; HEIDER, No. 38; GRABER, Nos. 28 and 30).

The most important recent details of the development of the brain in the Insecta have been given by PATTEN (No. 67) for *Acilius*, and by VIALLANES (No. 84) for *Mantis*. According to PATTEN, the whole head-rudiment shows signs of being composed of three segments (Fig. 160), this segmentation affecting not only the primary parts of the brain-rudiment, but also the rudiments of the optic ganglion and of the optic plates. On the three consecutive segments into which the optic plate (*op*) is thus divided, the rudiments of the six ocelli of the larva are distributed in *Acilius*, two ocelli occurring on each segment (Fig. 160 *A*, *1–6*). In the shifting of the separate parts of the rudiment of the head, which takes place at a later stage in connection with the development of the cephalic terga, as above mentioned (p. 302), changes occur in the position of the ocelli with regard to each other, but these we cannot here enter upon. The invagination above described also, which participates in the formation of the optic ganglion, is broken up, according to PATTEN, into three sections corresponding to the segmentation of the brain (Fig. 160 *B*, i^1, i^2); in *Acilius*, only the two anterior sections can be recognised as distinct invaginations, while the third is replaced by a solid ingrowth.

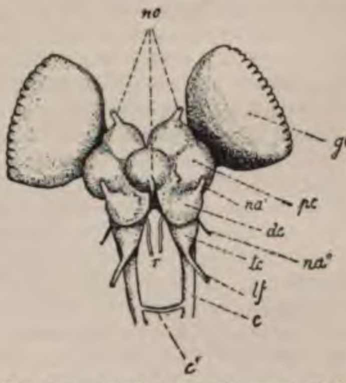

FIG. 161.—Anterior (ventral) aspect of the developed brain of *Oedipoda* (after VIALLANES). *c*, circum-oesophageal commissure; *c'*, transverse commissure behind the oesophagus; *dc*, deutocerebrum; *go*, optic ganglion; *lf*, labro-frontal nerve; *na'*, antennal nerve; *na''*, accessory antennal nerve; *no*, nerves of the three ocelli; *pc*, protocerebrum; *r*, root of the paired stomato-gastric ganglion; *tc*, tritocerebrum.

PATTEN's statements have been almost entirely confirmed by WHEELER (No. 95) in the case of *Doryphora*. CARRIÈRE's (No. 13) observations also seem to confirm Patten's views. Heider (No. 38) and Graber (No. 30), however, although convinced of the presence of a primary segmentation of the brain (b^1–b^3) in *Hydrophilus*, were unable clearly to recognise it in the optic ganglion and the optic plate. A comparison with the condition in other Arthropoda, especially in the Crustacea (Vol. ii., p. 162 *et seq.*), also supports the view that the optic ganglion is a secondary section of the brain belonging exclusively to the most anterior part. This view is in agreement also with the recent statements of Viallanes (No. 84) with regard to *Mantis*. According to this author, the primary part of the brain breaks up into three sections, corresponding to the *protocerebrum* (*pc*), the *deutocerebrum* (*dc*), and the *tritocerebrum* (*tc*) of the adult. Of these, the protocerebrum is connected with the optic ganglion (*go*) and also yields the nerves to the ocelli (*no*), as well as the dorsal integumentary nerves; the deutocerebrum yields the antennal nerves (*na′* and *na″*), while the tritocerebrum gives off the labro-frontal nerves (*lf*) which are connected with the frontal ganglion. In the rudiment of the optic ganglion, Viallanes could only recognise a division into an outer and an inner part (*premier lobe protocérébral* and *deuxième lobe protocérébral*). Cholodkowsky also (No. 20) observed the segmentation in the brain of *Phyllodromia*. He, however, considers the optic ganglia as belonging to the third segment of the brain.

The above considerations incline us to regard the primary cephalic region as being derived from three fused segments. Of these the most anterior would have to be called the true *primary cephalic segment*. The segment of the brain belonging to it (the protocerebrum) would be the homologue of the Annelidan brain derived from the neural plate. The second cephalic segment which we should have to identify with the *antennal segment*[*] would have to be regarded as a post-oral trunk-segment which has shifted forward secondarily (p. 295), and the third cephalic segment would also have to be regarded in a similar manner, being followed eventually by the hypothetical pre-mandibular segment and then by the mandibular segment.

Taking into account what has just been said, it must appear remarkable that, so far, observers have been able to find only one pair of coelomic sacs in the primary cephalic region (p. 320). This pair, according to Cholodkowsky, belongs to the antennal segment into the appendages of which it is prolonged. We should have to assume that the pair of primitive segments between these coelomic sacs and those of the mandibular segment have been secondarily suppressed.

It should be mentioned that the *frontal ganglion* and the *unpaired oesophageal nerve* connected with it are independent structures which only secondarily enter into connection with the brain. They owe their origin to an ectodermal invagination which belongs to the anterior wall of the oesophageal depression. This invagination yields the material for the formation of the frontal ganglion and the oesophageal nerves (Heider, No. 38; Carrière, No. 13).

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[*] It should be mentioned that Patten (No. 67) and Carrière (No. 13) reckon the antennae as belonging to the third brain-segment. [Bürger, in his work on *Chalicodoma* (No. II.), based largely on Carrière's notes, claims the antennae as belonging to the deutocerebral segment. A pair of minute evanescent appendages were found by Carrière on the protocerebral and another pair on the tritocerebral segment. It is thus evident, from his posthumous work, that Carrière had ceased to reckon the antennae as belonging to the tritocerebrum.—Ed.]

D. The Sensory Organs.

The Ocelli.

Detailed accounts have recently been given of the development of the *ocelli* by Patten (No. 67). There are, on each side, six ocelli which, according to Patten, are distributed in three pairs on what he assumes to be the three most anterior cephalic segments. The individual ocelli of these three pairs differ considerably from one another in structure and development, although a certain uniformity of type can be recognised. The fifth ocellus (the ventral ocellus of the third pair which, however, has shifted far forward in the larva)

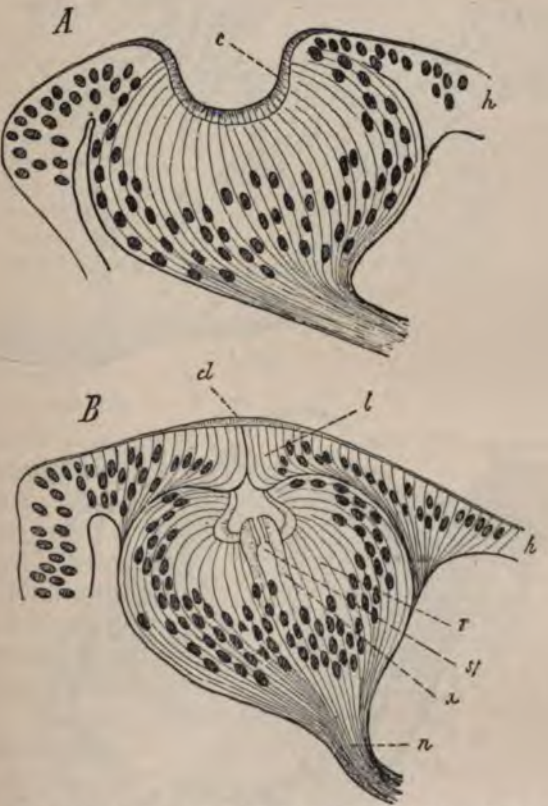

Fig. 162.—Two stages in the development of the fifth ocellus of an *Acilius* larva (after Patten). *c*, cuticular rods; *cl*, rudiment of the chitinous lens; *h*, hypodermis; *l*, lentigen layer (vitreous body); *n*, nerve; *r*, rudiment of the retina; *sp*, vertical slit in the retina; *x*, the retinal cells bordering this slit laterally.

approaches this common type the most nearly, and we shall therefore content ourselves by describing its development alone.

The rudiment of this ocellus (Fig. 162 *A*), at a certain stage of its development, strikingly recalls the simple *optic pits* or cup-shaped

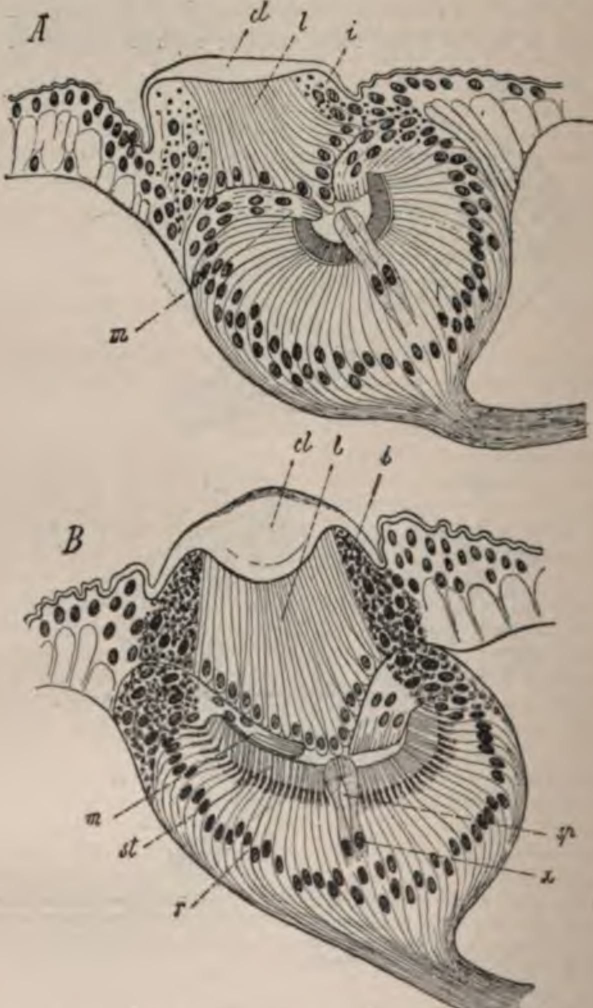

FIG. 163.—Two later stages in the development of the fifth ocellus of the *Acilius* larva (after PATTEN). *cl*, chitinous lens; *i*, so-called pigmented iris; *l*, lentigen layer (vitreous body); *m*, middle inverted layer of the eye; *r*, retina; *sp*, vertical slit in the retina; *st*, rods; *x*, cells bordering the vertical slit.

eyes found in certain Molluscs (*Patella*). It is a simple pit-like depression of a thickened part of the hypodermis. The elongate cells which compose the wall of this depression are arranged in a simple layer and, at their free ends, which are turned to the optic pit, carry a striated cuticular margin (*c*), while their inner or basal ends give off the nerve-fibres which unite to form the common optic nerve.

According to PATTEN, this apparently simple rudiment has arisen by the fusion of at least four distinct pits which represent primary embryonic organs, and in structure recall the eye-pits on the margin of the mantle in *Arca*. The nerve correspondingly shows its composition out of four originally separate bundles.

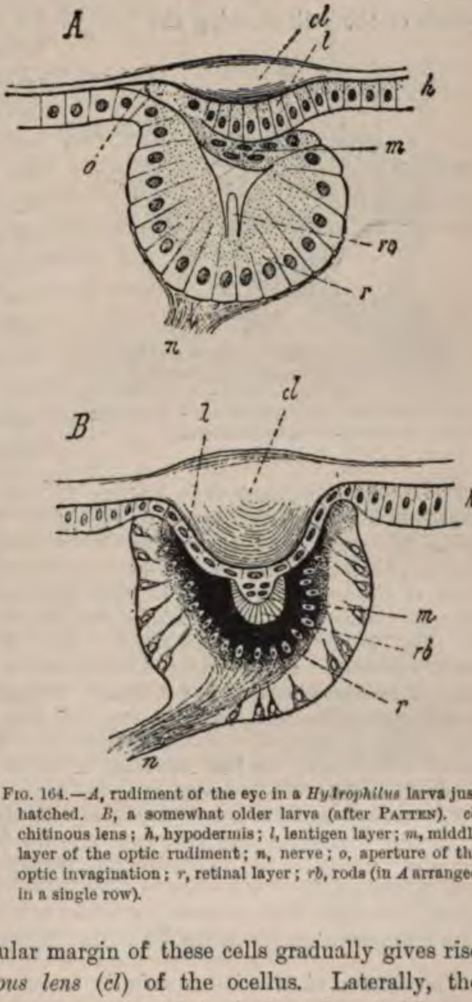

FIG. 164.—*A*, rudiment of the eye in a *Hydrophilus* larva just hatched. *B*, a somewhat older larva (after PATTEN). *cl*, chitinous lens; *h*, hypodermis; *l*, lentigen layer; *m*, middle layer of the optic rudiment; *n*, nerve; *o*, aperture of the optic invagination; *r*, retinal layer; *rb*, rods (in *A* arranged in a single row).

In later stages, the eye-pit closes towards the exterior (Fig. 162 *B*), the marginal parts pushing inward until they meet over the deeper parts. In this way the pit-like rudiment gives rise to an eye-cup which has by this process become *bilaminar*. The central part of the outer or superficial layer (*l*) becomes the *lentigen* layer (vitreous body), while the peripheral parts become the pigmented iris. The cuticular margin of these cells gradually gives rise to the cuticular *chitinous lens* (*cl*) of the ocellus. Laterally, the superficial layer of the eye passes direct into the hypodermis (*h*).

The deeper layer of the eye, which still retains its cup-like curve, must be considered as the rudiment of the *retina* (*r*). From its cuticular margin are derived the optic rods. Certain peculiarities characteristic of the eye of *Acilius* now develop. The chief of these is a slit traversing the retina perpendicularly (*sp*), which is bordered by the horizontally-placed rods of the large retinal cells (*x*) which lie next to it. In the further course of development (Fig. 163) a flattening of the cup-like cavity occurs, owing to the growth of the cells forming the base of the optic cup, and the rods belonging to these cells consequently assume a more vertical position. The retinal cells at the edge of the cup, on the contrary, curve inward and form an inverted marginal layer (*m*) with its rods directed towards the base of the retinal cup; these cells may be regarded as the rudiment of a third layer intercalated between the two principal layers of the eye.

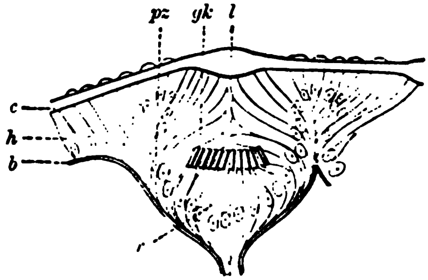

FIG. 165.—Section through the eye of a Coleopteran larva (*Dytiscus*) (after GRENACHER, from HATSCHEK'S *Text-book*). *c*, chitinous cuticle; *l*, corneal lens; *h*, hypodermis; *pz*, pigment-cells; *gk*, vitreous body; *r*, retina; *b*, basal membrane.

The above would justify us in deriving the bilaminar Insectan eye from a three-layered eye by the atrophy or incomplete development of the middle layer. The original presence of three layers in the ocellus is, according to PATTEN (No. 66), still more distinctly recognisable in the eye of the youngest larvae of *Hydrophilus* (Fig. 164), in which the optic invagination presses into the optic rudiment not from the middle, but from the edge and from the dorsal side (Fig. 164 *A*). Even in later stages a vestige of the middle cell-layer (Fig. 164 *B*, *m*) is retained. According to GRENACHER'S observations (No. 151), the ocelli of certain Insects appear to remain throughout life in a much more primitive condition than would be expected from PATTEN'S statements, the optic vesicle in them never closing completely, and the layers of retinal cells and of cells forming the lens remaining in direct continuity with the hypodermis (*e.g.*, Fig. 165).

The statements of PATTEN do not agree with those of CARRIÈRE (No. 14). If we rightly understand the latter author, in the development of the ocelli of pupae of *Chrysididae* and *Ichneumonidae*, the separation of the retinal layer from the lentigen layer takes place by delamination, while the optic invagination which forms later develops according to the type of the cup-eye, and at the same time stands in a certain relation to the development of the corneal lens.

The larvae of the holometabolic Insecta are, as a rule, devoid of compound lateral eyes (facet-eyes). These develop only in the gradual transition to the imaginal stage. The larvae, on the contrary, possess a number of laterally placed ocelli (very often six). The question now arises as to the relation of the compound lateral eyes of the imago to the ocelli of the larva. It is certain that the latter degenerate and are not taken over into the imago. In the pupa of the Lepidoptera, the degenerating ocelli can be seen detached from the hypodermis, and drawn back into the interior of the larva on the optic nerve as on a stalk (CARRIÈRE, No. 147). Since, at this time, the rudiment of the compound eye can be seen as a hypodermal thickening, it might be thought that the latter was altogether a new acquisition. But, according to PATTEN's observations on *Acilius*, there seems to be a certain relation between the larval and imaginal eyes. In *Acilius*, the highly developed and complicated larval eye (the first) has a peculiar dorsal appendage, which perhaps represents the vestige of an ocellus. The hypodermal thickening, which leads to the development of the imaginal lateral eye, develops first in the neighbourhood of this appendage. In later stages, this rudiment forms a thickened band which almost completely surrounds the six ocelli. This position perhaps favours a view which regards the complex of the six larval eyes and the compound eye that develops later merely as differently developed parts of one and the same optical area. We should here recall GRENACHER's view, according to which the ommatidia of the compound eye on the one hand, and the ocelli on the other, represent merely different ontogenetic forms and grades of development of one and the same type of eye (chap. xxviii.).

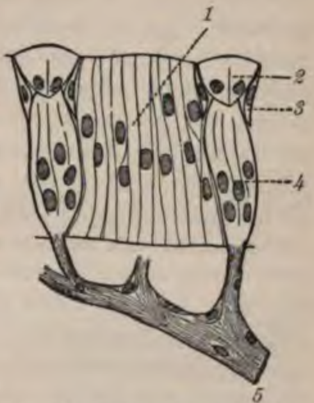

FIG. 166.—Section through the rudiment of the compound eye of *Vespa* (after CARRIÈRE, from HATSCHEK'S *Text-book*). *1*, cylindrical cells (later accessory pigment-cells); *2*, crystalline cone-cells; *3*, principal pigment-cells; *4*, retinulae; *5*, nerve, which gives off branches to the different ommatidia.

The frontal ocelli of the imagines of many Insecta have nothing to do with the larval ocelli. Against PATTEN's view that they may perhaps stand in nearer relation to the compound eyes we might adduce the independent condition of their innervation. These ocelli are often three in number. PATTEN (No. 66) observed in *Vespa* that the median unpaired ocellus is derived by fusion from a paired rudiment.

The details of the development of the *compound lateral eyes* (fan-shaped or facet-eyes) are so far chiefly known in connection with the pupae of the holometabolic Insecta (Diptera, WEISMANN, No. 129; Lepidoptera and Hymenoptera, CARRIÈRE, No. 147). In many cases, the first rudiment of the facet-eyes, as we saw above, is a paired lateral ectoderm-thickening, while in others, only a crowding together of the individual ectoderm-cells can be seen. The separation of the single ommatidia (single eyes) here takes place exclusively through histological differentiation (Fig. 166). At an early stage, as described in connection with *Mysis* (Vol. ii., p. 169), the single *ommateal pillars* and the undifferentiated tissue between them, which in *Vespa* form very massive *intermediate pillars*, can be distinguished. In the region of the *ommateal pillars* the cells become arranged to form two layers, the outer yielding the cells of the crystalline cone (*2*) and the principal pigment-cells (*3*), while the inner yields the retinulae (*4*), which are connected with the nerve-fibres (*5*). The cells of the crystalline cone secrete outwardly the cuticular corneal lens, while the crystalline cone develops within them in eyes of the eucone type. The cells of the intermediate pillars (*1*) give rise to the so-called accessory pigment-cells. In the course of further development the optic rudiment thickens considerably, the single ommatidia thus becoming taller and narrower, and also shifting closer together. The retinula-cells especially gain greatly in height. Pigment becomes deposited both in the retinula-cells and in the various pigment-cells which cover the outer side of each ommatidium. The development of the most essential features of the ommatidia seems to be thus completed (CARRIÈRE).

E. The Tracheal System.

The tracheae arise as paired, segmentally arranged ectodermal invaginations lying laterally to the limb-rudiments (Fig. 146 *A*, *st*, p. 295; Fig. 147 *A st*, p. 297; and Fig. 158 *E*, *tr*, p. 321). The tracheal invaginations are usually found developing at a somewhat early stage soon after the appearance of the limb-rudiments. It, however, appears from one of GRASSI's observations (No. 33) that, in *Japyx*, the tracheal system does not develop until a late embryonic stage. This would have to be regarded as the more primitive condition, recalling the Myriopoda (pp. 243 and 254). For since the tracheal system, phylogenetically considered, represents one of the latest acquisitions of the racial form, its early development in most Insects must be considered as being secondarily shifted back to early stages on account of its importance.

The originally simple tracheal invaginations (Fig. 158 *E*, *tr*) first widen at their bases, and then soon give off the tracheal branches as diverticula, while the narrowed aperture of the invagination is retained as the stigmatic branch and stigmatic aperture. The two longitudinal trunks of the tracheal system arise from the consecutive tracheal invaginations; these give rise to horizontally placed outgrowths, which grow out longitudinally until they meet and finally fuse with those of the next segment (BÜTSCHLI, No. 11). Only in late embryonic stages is the cuticular tracheal intima secreted. The tracheae become filled with air, according to WEISMANN (No. 87), to a certain extent even before the embryo hatches, the air being exuded, as it appears, from the tissues and the body-fluid.

The further development of the tracheal ramifications is brought about, as far as has yet been observed, by the continuous formation of diverticula. The branches which thus arise are therefore intercellular structures. On the other hand, it should be mentioned that the finest tracheal branches are intracellular canals. Although SCHÄFFER (No. 124a)* has correctly pointed out that the difference between these two methods of formation is not of any great importance, since in both cases there is merely an increase of surface (of a cell-plate in intracellular origin, or of a few cells in intercellular formation), the distinction has a certain interest when we compare the condition in *Peripatus*. The tracheae of *Peripatus* consist of numerous very fine tubes which, united to form a tuft, arise from a short funnel connected with the stigma. We may perhaps consider the fine tubes of *Peripatus* as equivalent to the intracellular and the funnel to the intercellular portion of the tracheal system of the Insecta.

At certain stages of development the tracheae bear a strong resemblance to the rudiments of the salivary glands† and the Malpighian vessels. This circumstance, as well as the position and number of these invaginations in the Hymenoptera, gave support to the view (held by BÜTSCHLI, No. 11, GRASSI, No. 32, and to some extent also by CARRIÈRE, No. 13) that we have in the tracheae and these glands homologous organs. If we consider the anatomy of *Peripatus*, we shall find that there are objections to this view. The apparently irregular distribution of the tracheae in *Peripatus*, and the facts that glands (salivary and excretory) similar to those of the Insecta and perhaps homologous with them are also present, show that the agreement in position and in number is of no consequence. Above all, however, the tracheae of *Peripatus* in structure differ greatly from the glands under consideration. Even MOSELEY'S view that the tracheae are transformed integumental glands, a view also held by PALMÉN, offers many difficulties. Apart from the circumstance that, in forms that stand nearer to the conjectural racial form of the Tracheata, integumental glands of this kind are not known to exist, the transformation of a secreting organ into an air-filled respiratory organ presupposes a change of function difficult to imagine. It is therefore most probable that we must regard the tracheal

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* Here also the literature on this point will be found.

† In the efferent portion of many spinning glands also a spiral thread altogether similar to that found in tracheae develops. But the fact that a similar spiral thread occurs also, for instance, in the vas deferens of the *Cytheridae* shows that no weight can be laid on this circumstance (KAUFMANN).

invagination as a structure *sui generis*. We may here point to the condition of the terrestrial Isopoda, in the branchial lamellae of which air-containing spaces altogether analogous to tracheae develop (*Tylus*).

F. The Alimentary Canal and Intestinal Glands.

Of the three sections of the alimentary canal, the **stomodaeum, enteron**, and **proctodaeum**, the first and third arise as ectodermal invaginations. In most cases the rudiment of the stomodaeum appears in the germ-band somewhat earlier than that of the proctodaeum (p. 294 and Fig. 145 *C*, *m*, p. 291). The musculature of these sections is yielded by the surrounding mesoderm. In the stomodaeal invagination an unpaired dorsal depression soon appears, from which are derived the frontal ganglion and the oesophageal nerve (p. 328).

The actual ectodermal character of the fore- and hind-guts has been established with considerable certainty by the unanimous testimony of observers, and by comparison with the conditions in other groups of Arthropoda. VOELTZKOW (No. 85), indeed, has recently derived both structures from the lower layers, and GRABER has adopted this view for the proctodaeum of *Musca*. With regard to this, we must refer to what has already been said (p. 315) as to the condition of *Musca*.

The connection between the cavities of the stomodaeum and proctodaeum with that of the enteron is usually established at a somewhat early embryonic stage. In certain larval forms, however (many Hymenoptera, *e.g.*, *Apis* and *Myrmeleon*), no communication is established between the enteron and the proctodaeum, the latter then having an exclusively excretory function.

The **enteron** develops from two originally distinct rudiments, the anterior and posterior entoderm-rudiments (p. 313), which from the very first bear a close relation to the invaginations of the stomodaeum and proctodaeum. Although originally applied as simple cell-accumulations to the inner ends of these invaginations, so closely, indeed, that VOELTZKOW (No. 85, 86), PATTEN (No. 68), and GRABER (Nos. 28 and 30) derived them directly from the epithelium of the latter, they soon extend, through continuous cell-proliferation, and assume the **U**-shape (Fig. 153 *A*, *en'* and *en''*).* The ends of the **U**-shaped rudiment in the anterior entoderm-mass are directed posteriorly, but in the posterior mass anteriorly. These ends grow out towards each other, meet and fuse, and thus form two paired entoderm-bands running dorsal to the germ-band along its whole length.

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* [As already stated (footnote, p. 317), HEYMONS (No. XX.) and LÉCAILLON (No. XXIX.) consider that the entoderm is quite wanting in the adults of the higher Insects, the mid-gut originating, according to these observers, as ectodermal ingrowths from the stomodaeum and proctodaeum.—ED.]

The paired entoderm-bands belong to the lateral parts of the germ-band. They lie, as a rule, immediately below the series of consecutive coelomic sacs (Fig. 158 *F*, p. 321), where the entoderm-bands (*en*) are seen cut through below (really dorsal to) the coelomic sacs (*us*). The dorsal wall of the primitive segments is thus in immediate contact with the entoderm-bands. Active proliferation of cells now takes place from this wall of the primitive segments, and the cell-material thus produced, which splits off from the dorsal wall of the primitive segments, forms the outer layer of the enteron-rudiment, the splanchnic layer or intestinal fibrous layer (Fig. 158 *F*, *spm*; Fig. 170, *sp*, p. 344). The remainder of the dorsal wall of the coelomic sac left after this separation enters into relation with the genital rudiment and yields the terminal filament (*cf.* p. 345, etc., and Fig. 170, *ef*). The entoderm-bands with the immediately contiguous splanchnic layer may now be termed the mid-gut rudiment (Fig. 150, *m*, p. 306, and Figs. 170, 171, 172, *sp* + *en*, pp. 344–346). In the following stages the enteron is distinguished for its great lateral growth, which causes it to spread over the surface of the food-yolk, which it finally completely surrounds (Fig. 150 *C–F*, p. 306, and Figs. 170–172, pp. 344–346). This circumcrescence, as a rule, occurs in such a way that the two entoderm-bands unite first in the region of the ventral middle line (Figs. 150 *E*, and 171). Only later do they unite on the dorsal side (Figs. 150 *F*, and 152). The food-yolk in this way comes to lie entirely within the enteron, and with it is included the remains of the dorsal tube or dorsal organ (Fig. 150 *F*, *s*) where such is present.

The description just given of the development of the enteron, which rests principally on the observations made on *Hydrophilus* and *Phyllodromia*, seems to be directly applicable to most Insects. In individual cases, indeed, we find certain deviations, as, for instance, in *Musca*, where the coelomic sacs do not attain distinct development (p. 320), and where the whole of the food-yolk is not taken into the enteron, a portion of it remaining (as in other Diptera) in the body-cavity where it is gradually absorbed (KOWALEVSKY, VOELTZKOW, GRABER). The conditions also differ to a certain extent in the Hymenoptera (*Apis*, *Chalicodoma*, KOWALEVSKY, GRASSI, CARRIÈRE), where the entoderm originally occupies a dorsal position (p. 316) and is only gradually grown over by the germ-band. The circumcrescence of the food-yolk by the entoderm here proceeds from the dorsal to the ventral side.

The **salivary glands** which open into the buccal cavity and may consist of several pairs* (*1–3*), arise as ectodermal invaginations

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* According to SCHIEMENZ (No. 125), the various cephalic glands of *Apis* (imago) are distributed in such a way that, originally, a pair occurs on each of the three maxillary segments.

which originally open, not into the stomodaeum, but on the surface of the body. . They may therefore be regarded as integumental glands, the apertures of which have been drawn into the buccal cavity (?). In the Trichoptera and Lepidoptera, an anterior pair of these glands develops in the anterior and inner angle of the mandibular rudiment (Hatschek, No. 36; Patten, No. 65). A second pair which here, as in the Hymenopteran larva, is transformed into spinning glands, belongs to the segment of the second maxillae (Fig. 143 *A*, *sp*, p. 286). Carrière, however, reckons it as belonging to the first thoracic segment. When the second maxillae fuse to form the lower lip, the apertures of the paired invaginations are approximated, and a short unpaired efferent duct forms, opening into the buccal cavity (Bütschli, No. 11, etc.).

We should be predisposed to homologise the salivary gland of the Insecta with the glands which open into the mouth in the Myriopoda. This view is opposed by the consideration that the latter, as transformed nephridia, are said to arise from the mesoderm (p. 251), while the salivary glands of the Insecta are purely ectodermal structures. We must therefore leave the question of the homology of these organs and of their relation to similar glands in *Peripatus* to be decided by further research.

The **Malpighian** vessels develop as paired outgrowths of the proctodaeum, which from the very first have a lumen. They are thus ectodermal structures. Two or three pairs usually make their appearance (Lepidoptera, *Phryganeidae*, *Hydrophilus*). In those forms which, at a later stage, have a larger number of these vessels, these secondary tubules develop as diverticula of the primary ones (*Gryllotalpa*, Rathke).

The Malpighian vessels usually appear only after the development of the proctodaeal invagination, as diverticula of this latter, but in the Hymenoptera (*Apis* and *Chalicodoma*), they form before the proctodaeum develops, as invaginations of the ectoderm, and consequently at first open on the surface of the germ-band. They then somewhat resemble in appearance tracheal invaginations, and this perhaps led to their being homologised with the latter, a view which we are unable to share, and which Carrière also (No. 13) did not adopt. Only later do they shift with the developing proctodaeal invagination into the interior of the embryo.

G. Heart.

The earliest recognisable rudiment of the *dorsal vessel* or *heart* in the Insecta appears as a longitudinal strand of cells (*cardioblasts*) running along the upper and external border of the dorsal subdivision of the primitive segments (Fig. 170, *h*, p. 344, and Fig. 171, *h*). During the continuous circumcrescence of the yolk by the germ-band, this rudiment shifts more and more towards the dorsal side. It is directly connected with the wall of the primitive segments (Figs. 170 and 171), and indicates the junction of the dorsal with the lateral wall of the coelomic sac. According to KOROTNEFF (No. 47), whom we have to thank for the first detailed account of the development of the heart in the Insecta, the cardioblasts are derived from the wall of the primitive segments.

In *Gryllotalpa*, the form described by KOROTNEFF, the condition is in many respects peculiar. The formation of the dorsal organ is here introduced, in the way described above (p. 304, etc.), by the rupture of the embryonic envelopes. The serosa contracts to form a thickened plate (Fig. 167 *A*, *rp*), of which the very degenerate amniotic folds appear as a lateral appendage (*am*), the whole being far removed dorsally from the edges of the germ-band (**x*–*y**) (*cf.* Fig. 150 *C*, p. 306). The interval between the rudiment of the amniotic fold and the lateral edge of the germ-band (**x*–*y**) is occupied by an epithelial lamella (*l*) in which we recognise the former amnion. This lamella is not closely applied to the yolk, but is separated from it by a spacious blood-lacuna (*bs*), in which can be seen numerous blood-corpuscles that have immigrated from the mesoderm. The cardioblasts which are derived from the wall of the primitive segment (*us*) have become arranged to form a channel (*gr*) on each side, and thus surround the lower part of the blood-sinus.

As the circumcrescence of the food-yolk by the germ-band progresses, after the invagination and degeneration of the dorsal plate has taken place, the two blood-lacunae fuse together dorsally to form one lacuna (Fig. 167 *B*, *bs*). This now represents the rudiment of the lumen of the heart. The two vascular channels, moving towards each other until they come into contact, form, by fusing together, the wall of the heart (Fig. 167 *C*, *r*, and Fig. 172, *h*, p. 346). The venous ostia arise, according to BÜTSCHLI (No. 11), as paired invaginations of the lateral walls, in the base of each of which a slit develops.

The rudiment of the heart, as we have seen, is intimately connected with the primitive segments. The lateral wall of the primitive segments, after giving off the elements of the somatic mesoderm, gives rise to an epithelial plate which represents the first rudiment of the pericardial septum or dorsal diaphragm (Fig. 167 *A*–*C*, *dd*; Fig. 170, p. 344; Fig. 171, p. 345, and Fig. 172, *ps*, p. 346). As soon as the two halves of the rudiment of the heart have united in the middle line, the two halves of the pericardial septum also become connected and bound the pericardial space, which is closed towards the rest of the body-cavity (Fig. 172, *ps*). For a time the pericardial septum remains connected with the wall of the heart, but it becomes separated from it later (Fig. 167 *C*, *dd*). The relations of the rudiment of the heart and the pericardial septum to the terminal filament of the genital rudiment will be discussed below (p. 345 *et seq.*).

The statements as to the development of the heart in the Insecta that have been made by other authors (Grassi, Patten, Tichomiroff, Ayers, Heider, Carrière, Heymons, etc.) can easily be traced back to the type described for *Gryllotalpa*. The principal difference in the formation consists in the absence or slighter development of the large blood-lacunae above described. The rudiment of the heart in the first stages is consequently of small extent, and can often hardly be recognised.

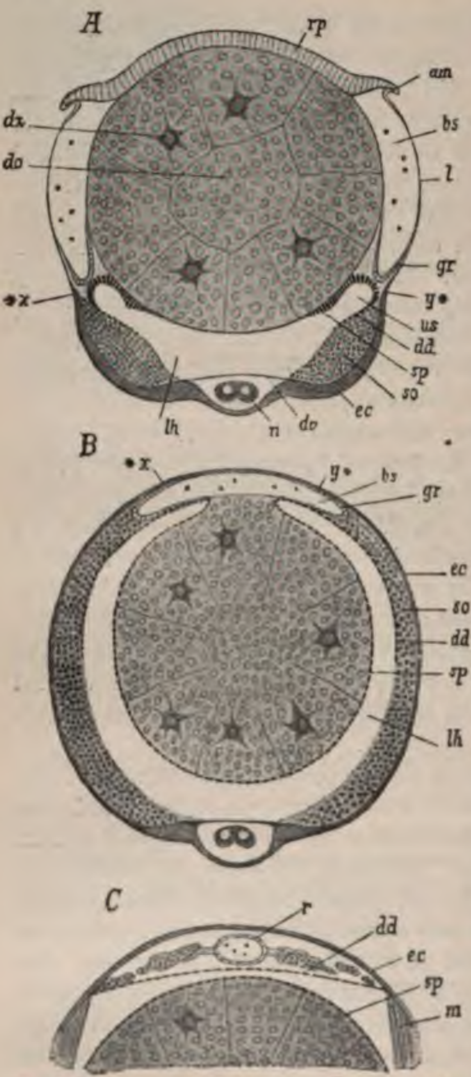

Fig. 167.—Diagrammatic transverse section through three consecutive stages of *Gryllotalpa* to illustrate the formation of the dorsal vessel (after Korotneff). (The rudiment of the fibrous layer of the intestine is omitted in these diagrams). *A*, youngest stage. The germ-band extends from *x to y*. The embryonic envelopes are rent and retracted dorsally. *am*, edge of the rent; *rp*, dorsal plate (serosa); *l*, lamella connected with the ectoderm of the germ-band (amnion reflected back). *B*, second stage. The germ-band has almost completely grown over the food-yolk. The dorsal organ is absorbed. *C*, third stage, dorsal region. The formation of the heart is completed. *am*, vestige of the amnion-fold; *bs*, blood-sinus; *dd*, rudiment of the dorsal diaphragm; *dv*, ventral diaphragm; *do*, food-yolk; *dz*, yolk-cells; *ec*, ectoderm; *gr*, vascular channel (rudiment of the heart); *l*, lamella of the reflected amnion; *lh*, permanent body-cavity; *m*, transverse muscle; *n*, ventral cord; *r*, heart; *rp*, dorsal plate; *sp*, splanchnic, *so*, somatic layer of the mesoderm; *us*, cavity of the primitive segment; *x-y*, lateral termination of the germ-band.

In *Gryllotalpa* and *Oecanthus* (AYERS) the posterior portion of the heart develops first. The order of development of the heart is here from behind forward. This is an unusual condition, which is due to the fact that the closing of the dorsal region is retarded by accumulated masses of yolk in the anterior part of the body.

[As in *Gryllotalpa*, the heart in *Agelastica* (PETRUNKEWITSCH, No. XXXVI.) and Bombyx (TICHOMIROFF, No. 78) is formed by the circumcrescence of the yolk by the mesoderm-bands. When these reach the mid-dorsal line, the two layers fuse immediately below the ectoderm, while they remain distinct below; in this way a mesodermal groove arises which, owing to the fact that the entodermal epithelium is still incomplete dorsally, is in open communication with the yolk. This constitutes the gastro-vascular canal of TICHOMIROFF, which, in transverse section, has the form of a figure 8. At this stage the dorsal and lateral walls of the heart are formed by mesoderm, while the incomplete ventral wall is entodermal. The entodermal epithelium now unites in the middle line, and thus completely separates the heart from the enteron and, soon after, the mesoderm grows in from either side towards the middle line below the cavity of the heart and above the entoderm, and finally, by fusion of the two ingrowths, the mesodermal walls of the heart are completed. The closure of the heart takes place earlier at the anterior and posterior ends than in the middle.—ED.]

The **blood-corpuscles** are traced back by KOROTNEFF to cells of the somatic mesoderm which have lost their connection with the rest of the mesoderm and have passed into the body-cavity. Our own [researches incline us to agree with this statement. Other authors, however (DOHRN, and recently WILL also, No. 97), have derived the blood-corpuscles from yolk-cells. AYERS (No. 1) even claims for their formation the cells set free by the disintegration of the dorsal plate. It should here be pointed out that SCHÄFFER (No. 124a) recently maintained that certain cell-complexes connected with the fat-body in caterpillars are formative centres for the blood-corpuscles (p. 372).

H. The Musculature, the Connective Tissue, and the Fat-body.

The groups of muscles, as well as the connective tissue, are derived through histological differentiation from the somatic layer of the mesoderm (Fig. 167, *so*). Our own researches, and those of KOWALEVSKY, GRASSI, and CARRIÈRE, show that the fat-body also arises from the mesoderm. In *Hydrophilus*, a dorsal band-like fat-body, running over the intestine, arises by direct transformation from the wall of the coelomic sac. For the rest of the fat-body also, for instance, for the lobes accompanying the tracheal system, a mesodermal origin can be indisputably established. The observations made by HEYMONS on *Phyllodromia* are in harmony with this. Certain cells of the wall of the coelomic sac early undergo a transformation, which results in their being recognisable as the rudiment of the future fat-body (Fig. 169 *B* and *C*, *f*).

Many authors, however, differ greatly as to the origin of the fat-body. DOHRN, TICHOMIROFF (No. 79), and, recently, WILL have derived it from the yolk-cells, while other authors have claimed an ectodermal origin for it. Among these latter are KOROTNEFF (No. 47) and SCHÄFFER (No. 124a), who, in confirming former statements made by WEISMANN, trace back the fat-body of *Musca* to growths from the tracheal matrix and partly from the hypodermis. GRABER also (No. 31) has recently maintained the ectodermal origin of the fat-body in *Hydrophilus* and *Stenobothrus*. As regards *Hydrophilus*, we are unable to agree in this view.

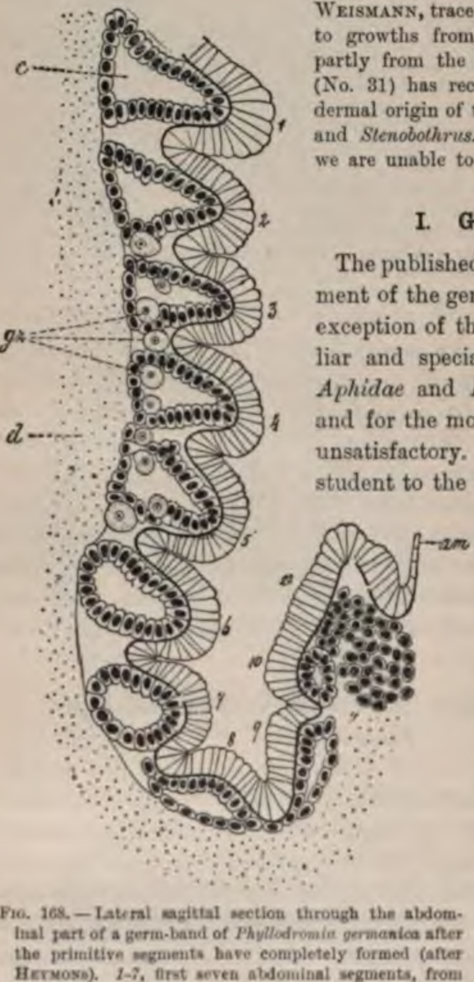

FIG. 168.—Lateral sagittal section through the abdominal part of a germ-band of *Phyllodromia germanica* after the primitive segments have completely formed (after HEYMONS). *1-7*, first seven abdominal segments, from the eighth (*8*) to the terminal segment (*es*) the abdominal germ-band is flexed ventrally; *am*, amnion; *c*, coelomic sac; *d*, food-yolk; *es*, terminal segment; *gz*, genital cells, lying partly in the dissepiments and partly in the wall or the cavities of the primitive segments.

I. Genital Organs.

The published accounts of the development of the genital organs are, with the exception of those relating to the peculiar and specialised conditions in the *Aphidae* and *Diptera*, much scattered and for the most part fragmentary and unsatisfactory. We must refer the student to the works of BALBIANI (No. 3), and WITLACZIL (No. 98), and especially to those of HEYMONS (No. 43). We are able, however, to gather (chiefly from the writings of GRASSI, No. 32, HEIDER, No. 38, and WHEELER, No. 95) that the genital glands are mesodermal in origin, and develop from the wall of the coelomic sac. The development of the efferent ducts has been best described by NUSBAUM (No. 61) and PALMÉN (No. 162). HEYMONS (No. 43) has recently published accounts of the rise of the genital organs in

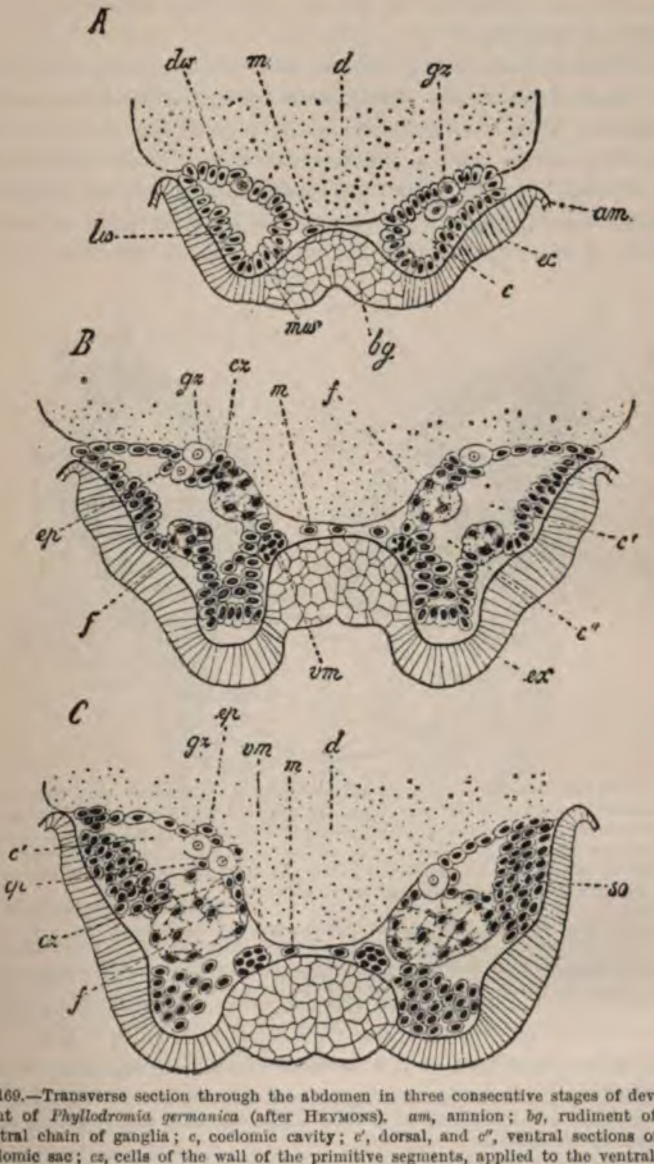

FIG. 169.—Transverse section through the abdomen in three consecutive stages of development of *Phyllodromia germanica* (after HEYMONS). *am*, amnion; *bg*, rudiment of the ventral chain of ganglia; *c*, coelomic cavity; *c'*, dorsal, and *c''*, ventral sections of the coelomic sac; *cz*, cells of the wall of the primitive segments, applied to the ventral side of the genital rudiment; *d*, food-yolk; *dw*, dorsal wall of the coelomic sac; *ec*, ectoderm; *ep*, epithelial cells; *ex*, abdominal limb-rudiments; *f*, rudiment of the fat-body; *gz*, genital cells; *lw*, lateral wall of the coelomic sac; *m*, mesoderm-cells, which do not take part in the formation of the coelomic sacs; *mw*, median wall of the coelomic sac; *so*, somatic mesoderm-layer; *vm*, ventral longitudinal muscle.

Phyllodromia germanica, on which, as the most detailed, we shall found our description.*

In *Phyllodromia*, distinct genital cells can be distinguished at an early stage of embryonic development by their different histological character. They are larger than the other cells, and show a slightly stainable nucleus with a distinct nucleolus. These genital cells, which have developed by the transformation of the embryonic mesoderm-cells, originally lie in the splanchnic layer or on the surface of this layer, which is turned towards the food-yolk at the boundaries of the segments. After the coelomic sacs are completely formed (Fig. 168, *gz*), they are found in the dissepiments which divide the consecutive sacs from one another. New genital cells continually develop here from mesoderm-cells. These cells develop in the second to the seventh abdominal segment.†

FIG. 170.—Transverse section through the abdomen in a somewhat older germ-band of *Phyllodromia germanica* (after HEYMONS). *bg*, rudiment of the ventral chain of ganglia; *c*, remains of the coelomic cavity; *cg*, rudiment of the efferent genital duct; *ec*, ectoderm; *ef*, terminal filament; *en*, entoderm; *fk*, fat-body; *gz*, genital cells; *h*, rudiment of the heart; *p*, rudiment of the pericardial cavity; *ps*, rudiment of the pericardial septum; *so*, somatic mesoderm; *sp*, splanchnic mesoderm.

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* The following description and figures were taken in advance from a treatise since published in the *Zeitschr. f. wiss. Zool.*, Bd. liii., kindly placed at our disposal by the author.

† [According to recent researches on the origin of the germ-cells in Crustacea and other Invertebrata, we should have to look for the first origin of these cells at an early cleavage-stage, at any rate, they should be visible as soon as the mesoderm-bands are formed. Further, we should not expect them to arise or to increase from the ordinary mesoderm-cells, but from germ-teloblasts.—ED.]

The genital cells shift later into the interior of the coelomic sacs, soon reaching their dorsal wall (Fig. 169 *A*, *gz*) and passing in between its cells. The coelomic sacs (*c*), in transverse section, at this stage are approximately triangular in outline, so that we may distinguish a dorsal (*dw*), a lateral (*lw*), and a median wall (*mw*). The dorsal wall is in contact with the surface of the yolk, and later, by delamination, yields the splanchnic mesoderm (Fig. 170, *sp*), while from its remainder is formed the *terminal filament* of the genital gland (*ef*). The lateral wall, which is parallel to the germ-band, takes an active part in the formation of the somatic layer (Fig. 169 *C*, *so*) of the mesoderm, the pericardial septum being eventually derived from what remains of it (Fig. 170, *ps*).

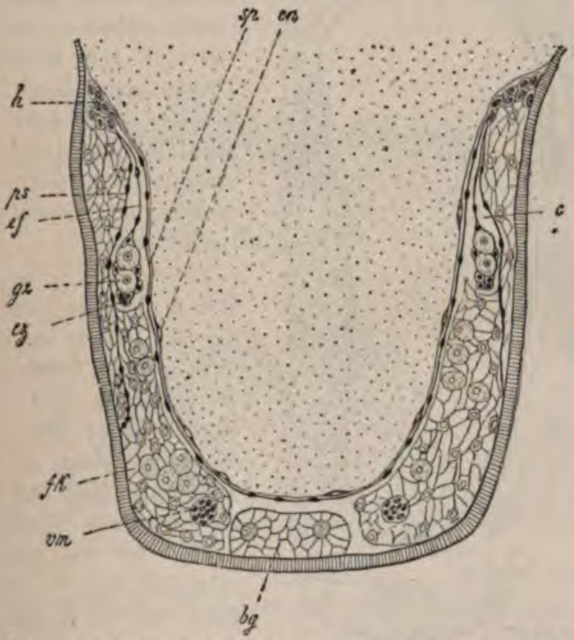

FIG. 171.—Transverse section through the abdomen in an older germ-band of *Phyllodromia germanica*, in the stage when the circumcrescence of the yolk commences (after HEYMONS). *bg*, ventral chain of ganglia; *c*, remains of the coelomic cavity; *cz*, rudiment of the efferent genital duct; *ef*, terminal filament; *en*, entoderm; *fk*, fat-body; *gz*, genital cells; *h*, rudiment of the heart; *ps*, pericardial septum; *sp*, splanchnic mesoderm; *vm*, ventral longitudinal muscle.

When the genital cells have entered the dorsal wall of the primitive segments, they are already so numerous as to form a continuous strand running from before backward. The genital rudiment then consists of a cell-strand lying on each side in the dorsal wall of the primitive segments, and extending from the second abdominal segment into the eighth. Not only genital cells take part in the formation of this strand, but undifferentiated mesoderm-cells (Fig. 169 *B*, *C*) are added; these originate in the dorsal wall of the coelomic sacs, and become closely applied to and in part surround the genital cells. These mesoderm-cells form the *epithelial cells* (*ep*) of the genital rudiment, while others compose a cell-strand (*ez*) lying medianly and ventrally to the genital cells.

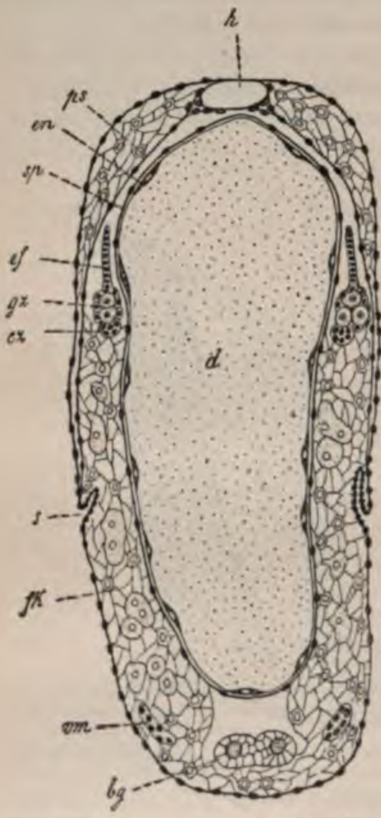

Fig. 172.—Transverse section through the abdominal region of an embryo of *Phyllodromia germanica*, after the circumcrescence of the yolk and the formation of the dorsal surface are completed. *bg*, ventral ganglionic chain; *ez*, rudiment of the efferent genital duct; *d*, food-yolk; *ef*, terminal filament; *en*, entoderm; *fk*, tissue of the fat-body; *gz*, genital cells; *h*, heart; *ps*, pericardial septum; *s*, tracheal stigma; *sp*, splanchnic mesoderm; *vm*, ventral longitudinal muscle.

The genital cells in the female give rise solely to the egg-cells (and to the nutritive cells, in those forms in which these occur). The follicular epithelium of the oviducts, on the contrary, as well as a corresponding cell-layer of the terminal chamber are yielded by the mesodermal epithelial cells.* *Phyllodromia*, to which the above description refers, and the Orthoptera generally, show in this respect a somewhat simple condition, the germ- or terminal chamber of the ovary consisting in them of comparatively few cells. In most other Insecta, and especially in those which have a great

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* [Each ovarian tube in the adult Insect consists of three parts: (1) the terminal filament, (2) a terminal chamber, often serving as a nutritive chamber, and (3) the actual ovarian tube divided into chambers, each containing an ovum; this last segment is much the longest.—Ed.]

number of nutritive cells in the ovary, the germ- or terminal chamber is extremely large. In this connection it has been maintained that the various cell-elements of the Insectan ovary originate from indifferent cells (**Korschelt**, No. 155, **Wielowiejski**, and others).

The ventral cell-strand (*cz*) becomes transformed in the proximal part of the oviduct, which widens into a cup and receives the separate ovarian tubes. The transformations which take place in the male will be described later.

The extent of the coelomic sacs, during the further course of development, becomes much restricted through the degeneration of those parts of them which extend into the limbs (p. 320), by the development of the fat-body (Figs. 169, *f*, and 170, *fk*), and through the separation of the somatic and the splanchnic mesoderm-layers (Fig. 170, *so*, *sp*). Only a small portion of them (*c*) finally remains, bounded laterally by the rudiment of the pericardial septum (*ps*), and internally by the terminal filament of the genital gland (*ef*). The dorsal region, where these two lamellae pass into each other, seems to be intimately connected with the cardioblasts (*h*). The strand-like genital rudiment now appears attached to the terminal filament as to a mesentery (Fig. 170, *gz*).

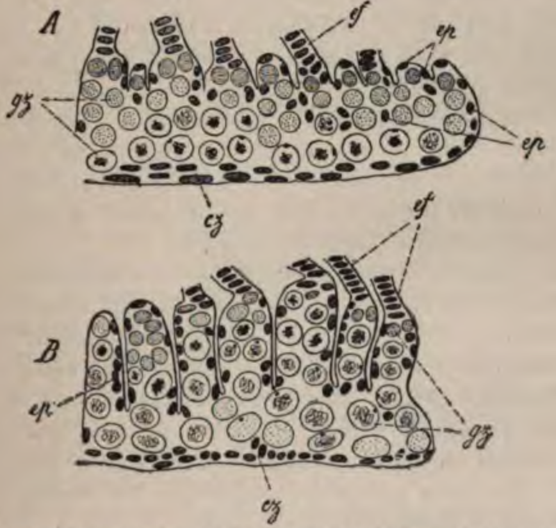

FIG. 173.—Longitudinal section through the female genital rudiment of *Phyllodromia germanica* (after **Heymons**). In *A*, the development of the ovarian tubes is beginning. In *B*, they have advanced further. *cz*, rudiment of the efferent genital ducts; *ef*, terminal filaments; *ep*, nuclei of the epithelial cells; *gz*, genital cells.

During the degeneration which takes place through the lateral circumcrescence of the yolk by the germ-band (Figs. 171, 172), the paired rudiment of the heart shifts more and more towards the dorsal median line, and the genital rudiment connected with it by means of the terminal filament follows it. This rudiment thus comes to lie on the dorsal side of the developing enteron (Fig. 172, *gz*).

The terminal filament (*ef*) originally represents a simple longitudinally-placed epithelial plate. A rearrangement of its cells soon, however, takes place, these becoming arranged in vertical rows, each of which corresponds to a developing ovarian tube. In this way the original plate-like terminal filament is broken up into the separate terminal threads of the ovarian tubes (Fig. 173, *ef*). In this process, however, the uppermost dorsal margin of the plate-like terminal filament does not participate, but persists as an undivided filament in the adult, where it is prolonged anteriorly and connects the different ovarian tubes; this is the so-called *Müller's thread*. The latter is originally connected with the pericardial septum, but at a later stage it appears to lose this connection.

As the separate ovarian tubes, which in *Phyllodromia* number about twenty, develop, they bend continuously inward from the dorsal towards the ventral side of the ovarian rudiment (Fig. 173). At the same time the epithelial cells (*ep*), some of which originally lay between the genital cells, become arranged so as to form an epithelium covering the surface of the ovarian tubes, this epithelium further secretes on its outer surface a structureless cuticular *tunica propria*. The outer peritoneal envelope of the ovaries is formed from the cells of the surrounding fat-body.

The genital rudiment originally, as we have mentioned, extended from the second into the seventh abdominal segment. In the latter, however, the genital cells are from the first few in number and completely disappear later, so that the genital strand here seems composed solely of epithelial cells. This part is the rudiment of the oviduct proper, and forms a direct continuation of the cell-strand (*cz*) mentioned above as lying ventrally to the genital cells, out of which, as we have seen, the proximal, cup-shaped portion of the oviduct is formed. The posterior section of the oviduct bends round towards the ventral side, and becomes connected with the hypodermis at the boundary between the seventh and eighth abdominal segments. The rudiment of the oviduct is originally a solid strand, in which a lumen forms later through the shifting apart of the cells.

In later stages the genital rudiment shortens considerably, so that it is then restricted to a smaller number of abdominal segments than at first. The separate ovarian tubes at the same time pass from their original vertical position and become more horizontal.

The paired insertion of the rudiment of the oviduct into the hypodermis of the intersegmental furrow between the seventh and eighth abdominal segments recalls conditions observed by PALMÉN in certain *Ephemeridae*, in which the paired aperture of the genital efferent ducts is retained throughout life. This is the original condition in the Insecta. In the female of *Phyllodromia*, the unpaired terminal section of the genital passage develops during larval life from an ectodermal invagination, a genital pouch forming in which the egg-cocoon is carried. This genital pouch is formed, as HAASE has proved, through the invagination into the interior of the body of the chitinous sternal plates of the eighth and ninth abdominal segments.

With regard to the development of the efferent genital ducts in the Insecta, we must refer to the results obtained by NUSBAUM (No. 61) and PALMÉN (No. 162), which fully agree with those here mentioned as obtained by HEYMONS for *Phyllodromia*.

NUSBAUM studied the **development of the efferent ducts** in *Pediculina* and *Periplaneta*. He found that only the vasa deferentia or the oviduct is derived from the posterior portions of the genital rudiment, *i.e.*, from mesodermal structures, while the rest of the efferent apparatus (uterus, vagina, receptaculum seminis, ductus ejaculatorius, penis, and all the accessory glands) develop from the integumental epithelium, and are therefore of ectodermal origin. The unpaired portions (the uterus, penis, receptaculum seminis, and unpaired glands) develop out of paired hypodermal rudiments. The posterior strands of the genital rudiments become applied to the hypodermal growths just mentioned and fuse with them. A fusion in the middle line of the paired hypodermal growths gives rise to the rudiment of the unpaired organs. These observations agree entirely with the results obtained by PALMÉN from the standpoint of comparative anatomy. PALMÉN found the most primitive type of efferent ducts in *Heptagenia* (an Ephemerid), an unpaired section being here altogether wanting. The oviducts open separately into the fold between the seventh and eighth abdominal segments, while the vasa deferentia open into a paired penis on the posterior margin of the ninth sternite. An unpaired section may develop from this paired rudiment in individual cases (♂ *Forficula*, MEINERT) through defective formation, one side atrophying after the paired terminal hypodermal growth has fused. In most cases, however, the unpaired terminal section must be regarded as a secondary integumental invagination. This point has not yet been investigated in all groups of the Insecta.

The agreement thus found to exist in the position of the genital apertures in *Phyllodromia* (Heymons) and in the *Ephemeridae* (which, according to Palmén, the *Perlidae* also resemble) may perhaps justify us in concluding that the opening of the genital glands on the boundary between the seventh and eighth segments corresponds to the primitive condition for all groups of the Insecta, and that the more posterior position of the apertures found in many forms has arisen secondarily by a backward displacement. If this is the case, we must assume that the condition in the Thysanura, in which the genital aperture is paired and opens between the eighth and ninth abdominal segments, or on the last, is a secondary modification (*cf.* Haase, No. 153).

The **external genital appendages** arise in most Orthoptera (as Dewitz has proved for the *Locustidae*) out of two pairs of cone-like projections belonging to the eighth and ninth abdominal segments, the posterior pair of which very soon become double. The six parts of the ovipositor of the female arise in this way, while, in the male, corresponding shorter projections are found. The ovipositor of the female *Ichneumonidae* and *Cynipidae* come under the same category, as well as the sting of *Apis* (Kraepelin, Dewitz, No. 103). Since the first rudiments of these paired appendages closely resemble the imaginal discs of the Dipterous larvae, they have repeatedly been regarded as abdominal limbs (p. 299, and footnote p. 300). The ovipositors of many Diptera and Coleoptera, on the contrary, as well as the penis of the Coleoptera, are to be derived from the most posterior abdominal segment, which is invaginated and telescopic.

The **male genital gland,** in *Phyllodromia*, at first develops in a way similar to that described above in connection with the female organs. Only in later embryonic stages can sexual differentiation be recognised. It is then found that, in the male, four accumulations of genital cells become surrounded with an epithelium. These accumulations, which represent the four testicular follicles of *Phyllodromia*, are closely connected with the rudiment of the efferent genital ducts (vasa deferentia), and, in later stages, shift with the latter somewhat backward and away from the original genital rudiment. A remnant of the genital rudiment still remains attached to the terminal filament, and this, according to Haase, is the female part of the originally hermaphrodite genital rudiment, and may, in individual cases, even develop imperfect ovarian tubes and eggs. It has yet to be proved that the vestigial organs found in the adult male have originated from this remnant of the genital rudiment.

Heymons concludes from the above observations that hermaphroditism was the original condition in the ancestors of the Insecta. This view, if correct, would account for the frequent occurrence of hermaphroditic conditions in adult Insects.

In the female, the whole rudiment of the primitive efferent ducts is directly transformed into the oviduct. In the male, on the contrary, the whole length of this rudiment does not become transformed into the vas deferens, but its distal terminal portion degenerates and is replaced by a secondary terminal section, which then becomes connected with the ectodermal ductus ejaculatorius.

If we pass in review the origin of the genital organs, as shown in the above description* of *Phyllodromia*, we have first of all to point out that, in the derivation of the genital cells from the epithelium of the coelomic sacs, we find direct agreement with the Annelida.† In the later development of the paired genital gland and of an efferent duct directly connected with it, there is a certain resemblance to the condition found in the Onychophora (p. 208). The dorsal position of the glands in these two Arthropodan groups is a special point of agreement. On the other hand, it should be pointed out that the genital gland of *Peripatus*, according to **Sedgwick**, arises by the direct fusion of the consecutive coelomic sacs (the Myriopoda have been placed in the same category by **Heathcote**, p. 252), and that therefore, in *Peripatus*, the genital cavity comes from the coelomic sacs. In the Insecta, on the contrary, the genital rudiment lies, indeed, in the wall of the coelomic sacs, but the lumen of the efferent duct here arises independently of the coelomic sacs, the cavities of the latter forming a small part of the permanent body-cavity. From this point of view, we shall have to regard the

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* The fact that this description not only applies to *Phyllodromia*, but is approximately applicable to many other Insects, perhaps to all, seems to be shown by the harmonious though fragmentary statements of **Heider** and **Wheeler** with regard to the Coleoptera.

† [It would seem highly probable, from recent researches on the origin of the germ-cells in various Invertebrata, that these cells, although not always to be distinguished by our limited vision from the general mesoderm, and especially from the coelomic epithelium, are in reality quite distinct from an early cleavage-period, and differ essentially from the mesoderm-cells in their nuclear organisation. This is rendered probable from the researches of **Hertwig** on *Sagitta*, **Haecker** on *Cyclops*, **Boveri** and others on *Ascaris*, **Weismann** on *Chironomus*.—Ed.]

condition in *Peripatus* and the Myriopoda as the more primitive, following directly on that of the Annelida, while the condition of the Insecta is, on the contrary, modified.

If we are to homologise the efferent genital ducts of the Insecta with those of *Peripatus*, we should have to trace them back to a pair of transformed nephridia. Their origin from the mesoderm in the Insecta would be in harmony with this; but, in other respects, we find no features retained in the development of the efferent genital ducts in the Insecta which can be considered as supporting such a view.

Mention should be made of **Heymons'** observations that, in the genital rudiment of *Phyllodromia*, the genital cells can from the first be distinguished from the epithelial cells. This statement is not favourable to the view, until now universally held, that the follicle-cells and egg-cells are derived from one and the same sort of cell by later differentiation. Regarding their first origin, however, in *Phyllodromia* also, the two kinds of cells are to be traced to the same source.

Special attention should be called to the fact that, in the Diptera and *Aphidae*, the genital rudiments can be recognised in a very early stage of embryonic life. This is certainly to some degree connected with the parthenogenetic and paedogenetic manner of reproduction, which is common in these two groups, and which (as in *Moina*, Vol. ii., pp. 123 and 180) leads to an early separation of the sexual rudiments.

In the Diptera, the first rudiment of the genital glands is represented by the "pole-cells." These cells (the "globules polaires" of **Robin**, also described by **Weismann** in *Chironomus* and *Musca*),* which become separated at the posterior pole of the egg even before the formation of the blastoderm, were discovered by **Leuckart** and **Metschnikoff** (No. 55) in the asexually developing egg of the viviparous larva of *Cecidomyia* (Fig. 174, *pz*). A rather large, highly granular cell (*pz*) here becomes severed from the posterior pole of the egg (Fig. 174 *D*) even before the blastoderm forms, and soon breaks up, first into two and then into four "pole-cells" (Fig. 174 *F*). When the blastoderm is completely formed, these "pole-

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* [It would be safer to discard **Robin's** term "globules polaires" for these cells, since that term was also applied by him and is still applied to the polar bodies or directive corpuscles, which latter, in all probability, have nothing whatever to do with the "pole-cells" of *Chironomus*, etc., which are simply the precociously separated germ-cells. This point, however, requires renewed investigation, and search should be made for the probable occurrence of true polar bodies and for the relationship of the "pole-cells" to the cleavage-nuclei. —Ed.]

cells" first shift between the blastoderm-cells (Fig. 174 *G*), and then into the interior of the embryo, where, in later stages, they become arranged symmetrically into two groups, and, surrounded by cells of the neighbouring tissue, become transformed into the genital rudiment (METSCHNIKOFF).

In *Chironomus* (Fig. 175), two "pole-cells" become constricted from the posterior pole of the egg almost simultaneously (BALBIANI), these, by division, yielding groups of four and eight cells. Just as in *Cecidomyia*, these cells are taken into the interior of the embryo (Fig. 175 *C*), and break up into two groups lying at the sides of the proctodaeal invagination. In quite young larvae that have hatched from the egg, these two spindle-shaped groups, the cells of which soon increase in number, can be recognised at the sides of the dorsal vessel, surrounded by a distinct membrane which, anteriorly and posteriorly, is continued into a ligamentous structure. The anterior corresponds to a terminal filament, the so-called *Müller's filament*. It is inserted into the dorsal vessel, and was held by SCHNEIDER (No. 74) to be muscular, this author consequently tracing back the genital rudiment of the Diptera to a transformed fibre of the alary muscle of the heart, an assumption which was refuted by

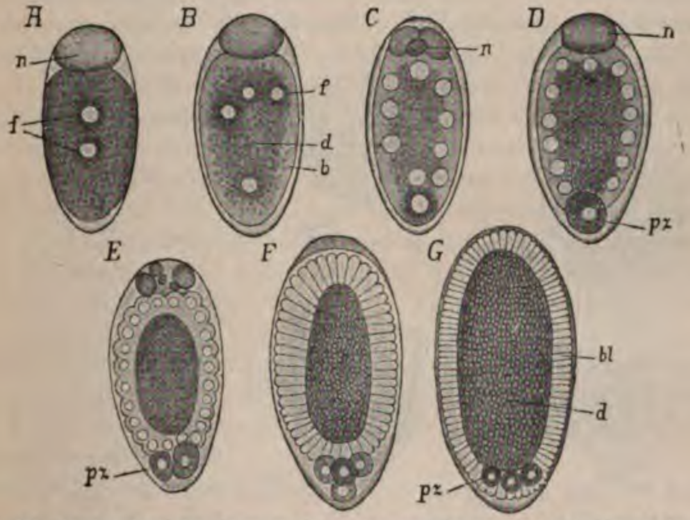

FIG. 174.—First ontogenetic stages in the parthenogenetic egg of the *Cecidomyia* larva (after METSCHNIKOFF). *b*, peripheral protoplasm; *bl*, blastoderm; *d*, central food-yolk; *f*, cleavage-nucleus; *n*, degenerating nutritive cells (the so-called corpus luteum); *pz*, "pole-cells."

BALBIANI. The posterior terminal filament is the rudiment of the paired efferent ducts of the genital gland. The division of the inner cells of the ovarian rudiment gives rise to rosette-like groups of cells, each of which corresponds to an ovarian tube. RICHTER's more recent accounts (No. 71) agree with the above statements of BALBIANI.

In the *Aphidae*, just as in the Diptera, the first rudiment of the genital organs becomes distinct at a very early stage. Even in those early stages in which the first rudiment of the amniotic cavity forms by invagination at the posterior pole (p. 279), and before the formation of the lower layer, a cell-group (the genital rudiment) severs itself from the wall of this invagination, and, as a paired rounded mass, comes to lie in the inside of the embryo. This cell-group, according to BALBIANI and WITLACZIL, is derived by division from a single cell. It becomes horseshoe-shaped, and breaks up into a number of rounded cell-accumulations, which become arranged in equal numbers on each side of the median plane of the body and represent the rudiments of the terminal chambers of the ovarian tubes. These cell-masses are enveloped in an epithelial cover which, anteriorly, passes into the terminal filaments and, posteriorly, into the efferent ducts. The origin of this epithelial covering is doubtful. The efferent ducts of the different ovarian tubes fuse on each side to form a common oviduct, and this is continued into an unpaired ectodermal invagination lying beneath the proctodaeum; this invagination gives rise to the accessory genital organs (METSCHNIKOFF, WITLACZIL, WILL).

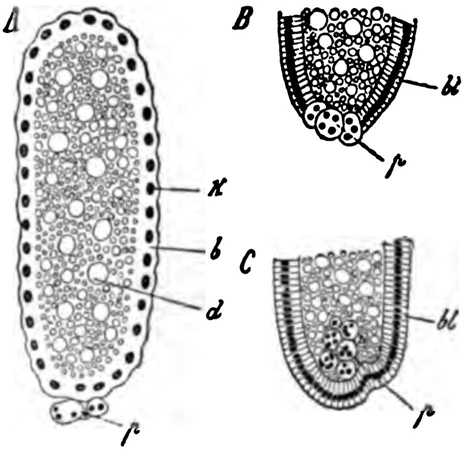

FIG. 175.—Three longitudinal sections through *Chironomus* embryos (after RITTER). In *A*, the "pole-cells" (*pc*) lie outside the developing blastoderm. In *B*, the pole-cells have pressed in between the blastoderm-cells. In *C*, they lie within the embryo. *b*, peripheral protoplasm; *bl*, blastoderm; *d*, food-yolk; *k*, nuclei of the blastomeres; *p*, "pole-cells."

II. Metamorphosis.

1. The Larval Forms.*

The Thysanura and the Collembola emerge from the egg in a form resembling that of the adult, so that there can here be no question as to the occurrence of a metamorphosis; they may consequently be described as true *Ametabola* (Insects without metamorphosis).

All other Insects, on the contrary, pass through a true metamorphosis. When they leave the egg they are distinguished from the adult not only by their smaller size, but also by the absence of the wings. Many Insect larvae differ further from the adult (*imago*) in a number of ways.

If we compare the young forms (*larvae*) of Insects when hatched with those of many Crustacea which leave the egg as *Nauplii*, we find a marked distinction between them. In the Insects, the typical number of segments is developed in the embryo; the limbs also, and the rudiments of the most important organs are already present. Only the wings are wanting. In other respects, the young emerging from the egg has the characteristics of a well-formed Insect. There is no doubt that the Thysanura, and among these the *Campodea* especially (Fig. 193), stand very near the fundamental form of this wingless larva. We have in the Thysanura undoubtedly the most primitive living representatives of the class of the Insecta. But we must not lose sight of the fact that, even amongst these forms, many systems of organs (*e.g.*, the tracheal system) have undergone reduction, possibly on account of the small size of the body.

The orders of the Insecta may be grouped in two divisions, according to the manner of their metamorphosis. To one of these groups belong those orders which we are accustomed to regard as the more primitive on account of their organisation; among these we find some with an invaginated germ-band, thus suggesting a connection with the Myriopoda. The larva here passes gradually, by a series of stages each marked by an ecdysis, into the imaginal form. During these stages the rudiments of the wings grow out, increasing in size gradually. Metamorphosis thus here takes the form of onward growth within the limits of the segmentation and rudimentary organisation already present. Such development is distinguished as *incomplete metamorphosis*, and the Insects belonging to this type are known as the *Homomorpha*.

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* In the following account we have chiefly followed LUBBOCK (No. 156) and BRAUER (No. 146).

The metamorphosis of the second group, to which the higher orders of the Insecta belong, is more complicated. The larva here leaves the egg in a condition which often differs considerably from that of the imago, not only in form, but also in manner of life. This larval stage, which is characterised by the large amount of nutrition taken, and repeated moults, attains a considerable size, and finally changes into a resting or pupal stage. The faculty of locomotion is now suppressed; the pupa hardly moves and takes no nourishment; all the animal processes step into the background, while the vegetative processes bring about the further (chiefly internal) changes in the body. The larval stage is thus followed by one which in many respects resembles the embryonic stages; the pupal stage might be defined as a recurrence of embryonic development. A certain distinction between the two is, however, evident to the careful observer. In the embryonic stages, the organs develop chiefly from uniform rudiments, whereas they are here often built up by the concrescence of a number of disconnected formative centres, the so-called *imaginal discs*. These imaginal discs must be regarded as persistent embryonic structures which have lasted throughout larval life in a latent condition, and in which the regenerative capacity of the embryonic rudiment has been retained. Those organs, on the contrary, which functioned in the larva undergo disintegration (p. 368).

The pupal stage gives place, after another moult, to the stage of sexual maturity, the winged imago-stage, during which there is no further growth of the body.

The Insects that develop according to this type are known as the *Heteromorpha*, and their metamorphosis is a *complete metamorphosis*, *i.e.*, they belong to the *Metabola* or *Holo-metabola*.

A. Homomorpha.

The post-embryonic development of the Insects belonging to this type is in most cases a true metamorphosis, in so far as the young animal that emerges from the egg, although similar in other respects, is distinguished from the adult by the absence of wings (and of those abdominal appendages which are transformed into the external genital organs). In some cases also, alteration in the manner of life may be accompanied by changes in the form of the extremities (*Cicada*). The transformation into the perfect Insect is gradual. The last larval stage, with the rudiments of the wings already developed, is known as the nymph or pupa. In the Pediculina and the Mallophaga alone, in consequence of parasitic life and the loss of the wings, metamorphosis is lost (acquired ametabole, LANG).

The Insects belonging to this type may be divided into two groups, according to the manner of their metamorphosis.

1. **Paurometabola.** The post-embryonic development is accomplished, through a series of moults, by the gradual growth of the body, of the wing-rudiments and the outer genital apparatus. This growth, though probably continuous, appears to be intermittent, being only visible at each moult. In Insects belonging to this group, the young stages resemble the adult, not only in form, but also in manner of life.

The Dermaptera, Orthoptera genuina, Corrodentia, Thysanoptera, and most Rhynchota conform to this type.

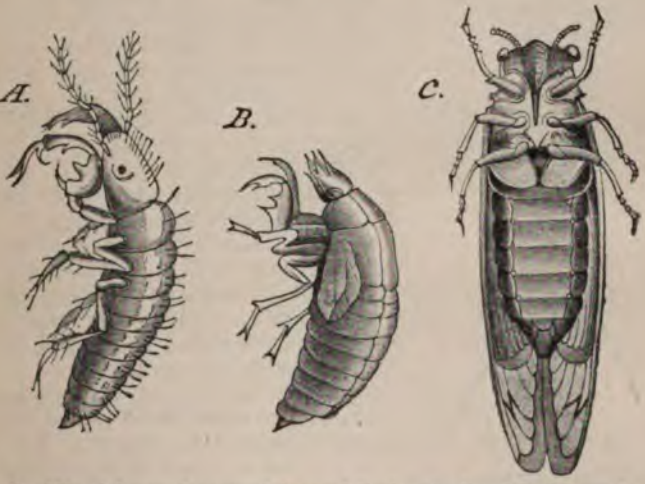

FIG. 176.—*A*, larva. *B*, pupa. *C*, imago of *Cicada septemdicem* (after PACKARD).

The young forms of most Rhynchota resemble the imagines in the structure of the mouth-parts and in the shape of the body, and change gradually into the adult form. The genus *Aleurodes* is an exception; its shield-shaped larva differs in appearance from the winged imago and passes into a resting, pupal stage, which is covered by the larval integument. There is here therefore complete metamorphosis. The same is the case in the male of the *Coccidae*, which changes into a resting pupa enclosed either in a protective larval integument or in a spun cocoon. The *Cicadidae* also (Fig. 176) attain a higher degree of metamorphosis. The larvae (*A*) live beneath the ground on the roots of trees, and are provided with hook-shaped fore-limbs adapted for digging. The nymph (*B*) is here capable of movement. Only shortly before the imago hatches does it remain quiet, while waiting for the bursting of the integument.

2. **Hemimetabola.** The young stage differs from the imago, not only in the absence of wings, but also in the presence of provisional (larval) organs.

The larvae live in water and differ from the imago in the condition of their respiratory organs, the former possessing tracheal gills, either external or internal (intestinal respiration) in position.

To this group belong the Ephemeridae, the Odonata, and the Plecoptera.

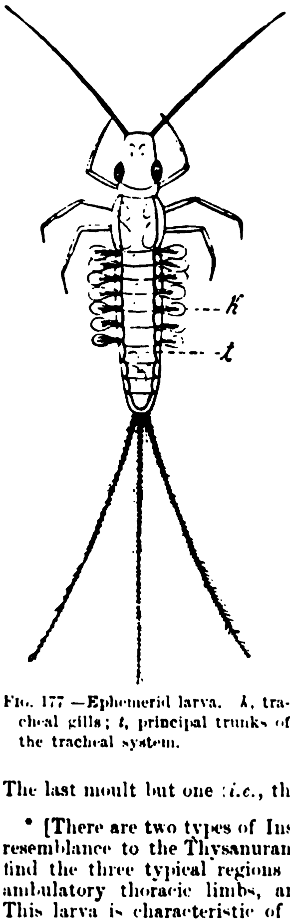

FIG. 177.—Ephemerid larva. *k*, tracheal gills; *t*, principal trunks of the tracheal system.

The Ephemeridae represent a very primitive group. In them alone have the paired efferent ducts of the genital organs been retained in their original form. The larvae (Fig. 177) live in water, and leave the egg in a Campodeiform stage.* In the later stages, they are distinguished by the possession of external tracheal gills (*k*), which may be leaf-shaped or tufted, etc., and are usually attached to the postero-external margin of the terga of the seven anterior abdominal segments. Within these integumental outgrowths, richly-branched tracheal trunks extend, and here the exchange of gases with the surrounding medium takes place. In keeping with the aquatic manner of life, the stigmata are closed, and the stigmatic tracheae found in the meso- and meta-thorax and in the eight anterior abdominal segments are merely thin strands quite devoid of air (*closed tracheal system*). Only at the moment of hatching do the stigmatic tracheae and the stigmata open, so as to allow of the passage of the tracheal intima which is shed with the body-cuticle (PALMÉN, No. 161). The number of moults which mark the successive stages through which the larva gradually approaches the imaginal form is very considerable (in *Chloë* over twenty, LUBBOCK). The last moult but one (*i.e.*, the last larval or nymph-stage) in which imperfect

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* [There are two types of Insect larvae: the Campodeiform, so-called from its resemblance to the Thysanuran *Campodea*, and the eruciform. In the first we find the three typical regions of the body clearly defined, biting mouth-parts, ambulatory thoracic limbs, and sometimes terminal abdominal appendages. This larva is characteristic of the Ametabola and the Hemimetabola. In the second type the head is usually well-defined, but the body-segments are simple and cylindrical, and the animal has a vermiform aspect, the mouth-parts are usually adapted for biting, but may be much reduced, the thoracic limbs are usually present together with functional abdominal appendages, the "prolegs." The eruciform larva is very generally found among the Heteromorpha; it attains its most characteristic development in the Lepidoptera, while in the Diptera it is much modified and degenerate, being apodal.—ED.]

wings are present, passes into a stage closely resembling the imago (*sub-imago*); this is distinguished from the preceding stages by the fact that, during it, no nourishment is taken. In this moult, the stigmata and stigmatic branches are definitely opened, and the tracheal gills, becoming constricted at their points of insertion, are cast off and remain in the empty skin (exuviae) of the last nymph-stage. One more moult on dry land leads from the sub-imago-stage to the form of the imago.

The larvae of the **Odonata** are in some cases elongate and very like the imago, in others they are distinguished from it by their more compact form. All Odonatan larvae are characterised by the remarkable modification of the lower lip which forms the protrusible "mask" (seizing pincer).

The respiratory organs are variously modified in the different genera. The closable stigmata on the thorax and abdomen of the larva (HAGEN) appear to be used chiefly for giving off air, but the older Libellulid larvae also breathe in air through the thoracic stigmata (DEWITZ). The tracheal gills are internal in *Aeschna* and *Libellula*, being situated as folds or outgrowths on the walls of the rectum (*intestinal gills*); in the *Agrionidae*, three branchial leaves are found on the last abdominal segment. These, as well as the intestinal gills of the *Libellulidae* (HAGEN), are cast off when the larva passes over into the imaginal form. In *Euphaea*, which is distinguished by the presence of abdominal appendages, long, conical gills are found on either side of the body near the stigmata on the second abdominal segment to the eighth (HAGEN).

Plecoptera. In so far as, in the *Perlidae*, the tracheal tufts (Fig. 178 *A*, *k*) are retained in the imago, and the actual metamorphosis consists only of the gradual growing out of the wings, this family, strictly speaking, should be classed among the Paurometabola. The larvae are Campodeiform (Fig. 178 *B*) and their respiratory organs appear in various positions, as lateral gill-tufts (Fig. 178 *A*, *k*) at the sides of the thorax, as pro-sternal gills on the first ventral shield, at the sides of the anal aperture, or on the lateral margins of the abdomen. We are justified in classing the *Perlidae* among the Hemimetabola, by the fact that the branchial tracheal gills in the imagines do not function as such, but are retained in a shrivelled and vestigial condition.

B. Heteromorpha.

The larvae of the Insects that belong to this group are very different in appearance from the imagines. Some of them recall the Campodeiform larva, but they are often modified in adaptation to a definite manner of life, and frequently degenerate through the preponderance of the vegetative functions and the partial suppression of free locomotion in consequence of more or less parasitic life. The climax of degeneration is reached in the limbless and eyeless "maggot" with reduced masticatory organs. In most cases the larva differs entirely from the adult in its manner of life. We must regard complete metamorphosis as a more specialised form of the process of development, an acquired differentiation in larval life distinguishing the highly-developed, but probably, according to their origin, younger orders of Insects as contrasted with the Homomorpha.

The last stage of larval life is always the *pupal stage*, which, in the form of the body, the development of the limbs, and the structure of the mouth-parts, resembles the imago. In this stage the Insects cease to take nourishment, and also, as a rule, the capacity of locomotion is lost (quiescent or resting pupa). The pupa is often enclosed in a cocoon spun by the larva. If the limbs of the pupa stand out freely from the surface of the body it is known as free-limbed (*pupa libera*, the *exarate*, *incomplete*, or *sculptured pupa*). In other cases the limbs which, in the resting pupa, are held closely pressed against the ventral side, become free immediately after the casting of the larval integument, but soon become glued to the surface of the body by the hardening of a tough secretion, so that their outlines are less distinct (Lepidoptera and many Diptera). Such forms are known as *mummy pupae* (*obtected*, *larvate*, or *signate pupa*, *chrysalis*). Among the Diptera it often happens that the pupa remains surrounded by the last larval integument (*barrel-like pupa*, *pupa coarctata*).

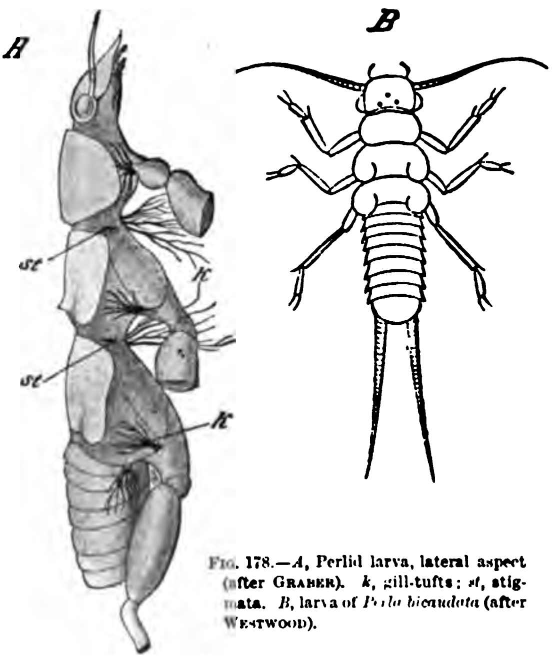

FIG. 178.—*A*, Perlid larva, lateral aspect (after GRABER). *k*, gill-tufts; *st*, stigmata. *B*, larva of *Perla bicaudata* (after WESTWOOD).

The number of moults undergone by an insect with complete metamorphosis is limited, and never attains that found among the Homomorpha (*Ephemeridae*).

Neuroptera. The larvae of the *Sialidae*, which in appearance resemble many Coleopteran larvae, have mouth-parts adapted for biting, like those of the imago. The larvae of the Megaloptera, on the contrary, have their mouth-parts singularly transformed for sucking the juices of their prey; the mandibles have a furrow on the lower side, and, with the maxillae, form on each side a sucking tube. Some of these larvae are elongate and recall the Coleopteran larvae

(*Mantispa*, the remarkable form *Sisyra* which is parasitic on *Spongilla*), while others have a short and more compact body (*Myrmeleon*). We find here a rare phenomenon, the substitution in the imago of biting mouth-parts for the sucking mouth-parts of the larva, which also occurs in the *Dytiscidae* among the Coleoptera.

The pupa is essentially quiescent and free-limbed; in the Megaloptera it lies enclosed in a coarse-meshed, rounded cocoon. In some forms, however, immediately before changing into the imaginal form, it becomes capable of locomotion and wanders about before casting the pupal skin. In this condition we find a transition to the metamorphosis of the Paurometabola with nymphs capable of movement.

Panorpatae. The larvae are eruciform and live beneath moss or underground. The head is heart-shaped and the mouth-parts strong and adapted for biting. There may be eight pairs of ventral feet (on the first eight abdominal segments). At the end of the abdomen there is the rudiment of a pair of anal forceps which recalls that of the *Forficulidae.* These larvae are distinguished from similarly-shaped Lepidopteran and Hymenopteran larvae by the possession of compound eyes composed of closely crowded ocelli.

Trichoptera. The Phryganeid larvae live chiefly in water in cases constructed by them out of foreign bodies (stones, parts of plants, snail-shells); these are in some cases attached to stones. In appearance (Fig. 179) they resemble the Coleopteran larvae. They have three pairs of long thoracic limbs, and at the end of the abdomen a pair of processes beset with hooks (*h*). At the sides of the abdomen (and of the meso- and meta-thorax) tracheal gills (*k*) are found in the form of tubes or tufts. The pupa is free-limbed; the pupal stage is passed through within the larval case after another envelope has been spun within it. Before the imago emerges, the pupa becomes capable of locomotion, leaves the pupal envelope and creeps on to dry land, where the transformation takes place.

FIG. 179.—Larva of *Phryganea fusca* (after PICTET). *h*, grasping hooks; *k*, tracheal gills.

Lepidoptera. The larvae here all agree in appearance and take the form of caterpillars (*eruciform*). Most of them live on land; only a few *Pyralidae* spend their larval life in water. In these latter, tubular tracheal gills may develop (*Paraponyx; Acentropus, Hydrocampa*, and *Cataclysta*, on the contrary, are devoid of true tracheal gills). The most anterior of the thirteen externally recognisable rings of the body represents the cephalic complex of segments. It carries the usually three-jointed, short antennae and the biting mouth-parts. A line running in the median plane, and known as the fork-line, corresponds to the growth-suture of the cephalic lobes. On the two sides of the head are found six (less frequently five) ocelli arranged in a semicircle. The three thoracic rings which follow after the head resemble in form the abdominal rings. The first pair of stigmata belongs to the pro-thorax, the eight subsequent ones to the first eight abdominal segments. The limbs are rarely altogether wanting (*Micropteryx* among the *Tineidae*); in other cases they are vestigial (a few burrowing caterpillars). Usually, three pairs of short, jointed thoracic limbs and five pairs of abdominal limbs are present. The latter are found on the third to the sixth abdominal segment, and on the terminal segment as the so-called prolegs. They are truncated, and have a bilobate or circular sole beset with minute hooks. In *Nepticula*, there are in all eighteen limbs. In other cases, the number is diminished by the reduction of the abdominal pairs, in some caterpillars, only two or three abdominal pairs of limbs being found (on the sixth to the ninth abdominal segment) besides the three thoracic pairs.

The pupa is a mummy pupa (*pupa obtecta*), and is frequently enclosed in a cocoon. In a few *Tineidae* (especially in *Micropteryx*), the limbs are said to be partly free. The mouth-parts in their structure essentially resemble those of the imago.

Diptera. The larvae of the Diptera must in general be regarded as essentially degenerate forms. The variation found in the different sub-groups is all the greater on this account. We have here the best examples of the type of limbless, soft-skinned "maggots," whose body consists of a number of similar rings. Functional thoracic limbs are always wanting, and vestiges are only found on the first thoracic segment. In the same way, truncated ventral feet occasionally develop on the abdominal segments. The mouth-parts also are often quite vestigial. In most cases the integument is soft, but it may be of a firmer character (*Stratiomys*, in the larval skin of which, according to LEYDIG, lime salts are deposited). The soft constitution of the integument may also extend to the cephalic segments (*headless larvae*); at this part, as a rule, however, a chitinous oesophageal framework develops, or a more or less marked maxillary capsule. But only in those cases in which this chitinous capsule contains the cephalic ganglia is it designated as the actual "head" (BRAUER, *eucephalic larvae*).

The pupa is not always quiescent. In individual cases (*Culicidae*) it moves about in the water by the contraction of the abdomen. The resting pupa is often enveloped in the larval integument, and is then known as the barrel-shaped pupa. It is either free-limbed (*pupa libera*), or, like the Lepidopteran pupae, is provided with limbs glued to the body (*pupa obtecta, mummy pupa*).

The forms assumed by the Diptera larvae are utilised by BRAUER (No. 100) for systematic purposes. He distinguishes two principal types, according to the manner in which the larval integument splits before the pupal stage is entered upon (or, in cases in which a barrel-like pupa is formed, when the imago hatches): (1) the *Orthorhapha*, in which, as a rule, a longitudinal slit opens on the back and a transverse slit at right angles to it; (2) *Cyclorhapha*, in which the slit is a circular one, transverse to the long axis of the pupa, so that one or two caps are pushed off at the anterior pole. To the first type belong the eucephalic larvae of the *Culicidae* and *Chironomidae*, and further the larvae of the *Tipulidae*, *Cecidomyiidae*, *Stratiomyidae*, etc., while the *Muscidae*, *Syrphidae*, and *Pupipara* belong to the second type.

Great variety prevails with regard to the condition of the respiratory organs. Many larvae breathe only through the last pair of stigmata at the posterior end of the body which have remained open (*metapneustic respiration*), in others a pair of anterior pro-thoracic stigmata remain open in addition to the posterior pair, while the others are closed (*amphipneustic respiration*); again, in other cases, some of the intermediate stigmata are also partly open (*peripneustic respiration*). The pupae of many forms, on the other hand, breathe only through the most anterior pair of stigmata which occur on the pro-thorax (*propneustic respiration*).

Siphonaptera. The larva is limbless, has biting mouth-parts, and consists of a head and twelve more or less similar segments. It has ten pairs of stigmata on the three thoracic and the seven anterior abdominal segments. The pupa is free-limbed. The mouth-parts and the form of the body resemble those of the imago; it lies in a cocoon.

Coleoptera. Many Coleopteran larvae are Campodeiform. They have three well-developed pairs of limbs on the thoracic segments and, at the end of the abdomen, in many cases, there is a pair of filamentous or stylet-shaped appendages. More frequently a pair of truncated prolegs is found at the posterior end of the body. The head, which is always well developed, shows the fork-line mentioned in connection with the Lepidoptera, and carries antennae, which are usually short, and a variable number of ocelli (six or fewer) on each side; these, however, are often wanting. The mouth-parts are adapted for biting, the mandibles are, in individual cases (*Dytiscidae*), changed into sucking organs. There are generally nine pairs of stigmata, the first of which occurs on the first or second thoracic segment, or on the boundary between the two, while the others belong to the first eight abdominal segments. The aquatic larvae (*Dytiscus*, *Hydrophilus*) are metapneustic, some having tracheal gills (*Gyrinus*). The body may be elongated as in the thread-like larva of the *Elateridae*; in other cases, it broadens out into a shape resembling the Isopoda (*Parnidae*). The Lamellicorn larvae are eyeless, soft-skinned, and whitish in colour, and are further distinguished by the sac-like enlargement of the last ring of the body (*Rhizotrogus*). In forms which bore their way into wood or under the bark of trees, the limbs are vestigial or are altogether wanting (*Buprestidae*, *Cerambycidae*). Such degenerate larval forms may finally become maggot-like (*Curculionidae*, *Bostrychidae*).

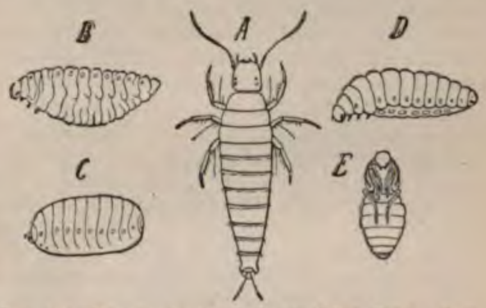

FIG. 180.—Metamorphosis of *Sitaris* (after FABRE, from LUBBOCK). *A*, first larval stage. *B*, second larval stage. *C*, third larval stage (so-called pseudo-chrysalis) *D*, fourth larval stage. *E*, pupa.

The pupa is free-limbed, and resembles the imago in the form of the body and in the structure of the mouth-parts.

A complicated metamorphosis, named by FABRE (No. 105) hyper-metamorphosis, is undergone by the *Meloidae* in adaptation to the peculiar manner of life of the larva. The young is at first an active Campodeiform larva (Fig. 180 *A*), which attaches itself at the first opportunity to the male of *Anthophora*, and, during copulation, passes over to the female. As soon as the host has laid its eggs in the cell prepared for them in the earth and filled with honey, the *Sitaris* larva takes possession of the cell, devours the egg, and subsequently lives upon the honey. Here it moults and passes into a stage in which it can only move slightly, and is maggot-like with reduced limbs (Fig. 180 *B*). It then changes into a pseudo-chrysalis (Fig. 180 *C*), a quiescent, pupa-like stage. From the pseudo-chrysalis there emerges first a larva resembling the second stage (Fig. 180 *D*), and then the actual pupa (Fig. 180 *E*), which changes into the imago. The freely moving as well as the resting stages are thus here multiplied.

Hymenoptera. The larvae of the Hymenoptera belong to various types. The larvae of the *Tenthredinidae*, which feed upon leaves, in appearance and colouring resemble the Lepidopteran larvae, and are therefore called **false caterpillars** (Fig. 181). They are distinguished from true caterpillars by the possession of a single ocellus on each side of the head, and by the unusually large number of abdominal limbs, the anterior pair belonging to the second, and not, as in the true caterpillars, to the third abdominal segment. There are generally six to eight pairs of abdominal appendages. An exception is afforded by the genus *Lyda*, in which, besides the thoracic limbs, there is only a pair of jointed appendages (*cerci*) at the posterior end of the body. These false caterpillars resemble the larvae of the *Uroceridae*, which bore into wood, but the latter are distinguished by the absence of eyes and of abdominal limbs. Most of the other Hymenoptera have degenerate larval forms in consequence of their peculiar and often parasitic or semi-parasitic manner of life. Whether the larva develops in vegetable outgrowths (galls), like many *Cynipidae*, or parasitically in other Insect larvae, like some *Cynipidae*, the *Pteromalidae*, *Ichneumonidae*, etc., or whether it finds nutritive material in the cells constructed and stored with food by the parent, or is fed during growth (Fossoria, *Vespidae*, *Apidae*, *Formicidae*) the passivity connected with its manner of life always brings about a reduction of the limbs and of the mouth-parts, and an approximation to the general appearance of the maggot. In the larvae of Bees and Wasps, the enteron remains closed posteriorly, and does not communicate with the proctodaeum which receives the Malpighian vessels. The pupal stage is generally passed through within a spun cocoon. The pupa is free-limbed, and resembles the imago in structure, since, when the larva passes into the pupa, the limb-rudiments are only gradually protruded from the imaginal disc (pp. 371-374), the pupal stage is preceded by a form showing the limbs only half protruded (DEWITZ, No. 102), and it is this form that is known as the semi-pupa, sub-nymph, or pro-nymph.

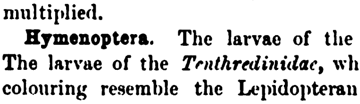

FIG. 181.—Eruciform larva of a Tenthridinid (*Trichiosoma lucorum*, after WESTWOOD).

The eggs of the *Ichneumonidae*, *Braconidae*, and *Pteromalidae* develop in the eggs or larvae of other Insects. The larvae of the *Ichneumonidae* are, as a rule, maggot-like. They may, however, possess at the posterior end of the body caudal appendages (*Anomalon*) or caudal vesicles (*Microgaster*), which are lost on entering the pupal stage. The *Pteromalidae*, on the contrary, undergo a very remarkable metamorphosis. The ontogeny of these forms which has been described by FILIPPI, METSCHNIKOFF, GANIN, AYERS, and LEMOINE, is characterised by the absence of nutritive yolk from the egg, by the absence or imperfect development of the embryonic envelopes, by the early hatching of the larva, and by the strange shapes of the larval forms. We are still very much in the dark as to the first stages of development. In *Platygaster*, a continuous process of division gives rise to numerous cells, some of which soon become arranged to form a superficial layer which surrounds the embryo in the form of an envelope (corresponding to the serosa). The other cells form the rounded embryonic rudiment, in which an outer ectodermal layer and an inner (lower) layer can soon be distinguished. The embryo now lengthens and is soon divided by means of a groove which sinks in ventrally into an anterior widened cephalic section and a posterior narrowed section. The stomodaeum appears as an ectodermal invagination in the cephalic section, and soon becomes connected with the enteron which has developed from the inner cells. The proctodaeum arises considerably later, and does not communicate with the enteron until a very late stage. In the cephalic section (Fig. 182) a pair of grasping hooks (*kf*) develop at the sides of the mouth, and behind these a lower lip (*ul*). Another pair of limbs (*lfg*) arise later at the posterior boundary of the anterior section, and a pair of short antennae (*a*) develop anteriorly. The posterior section of the embryo becomes divided up into several segments and runs out into a fork-shaped appendage (*f*) recalling the furca of the Copepoda. On this account the first larval stage that hatched from the embryonic integument after the hardening of the chitinous cuticle, was known as the *Cyclops*-like stage (Figs. 182 and 183). It appears that, in this stage, only the intestinal canal and the limb-muscles have been differentiated, while the other still undifferentiated organs

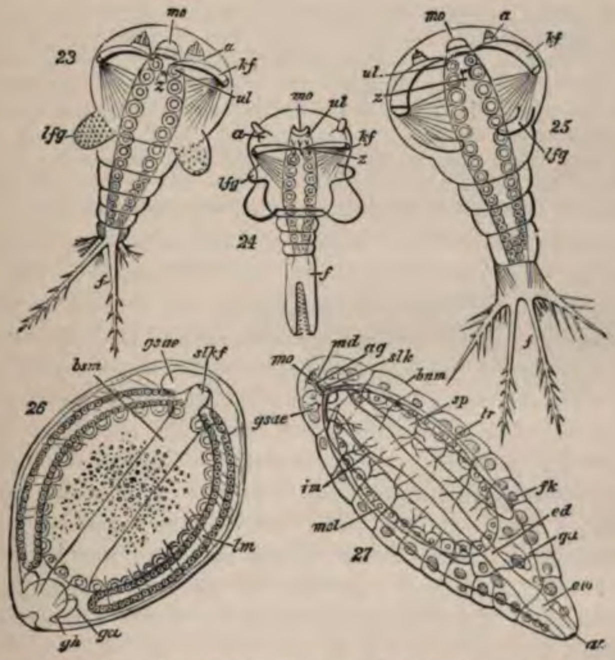

FIG. 182.—Stages in the development of *Platygaster* (after GANIN, from LUBBOCK). 23, 24, 25, so-called *Cyclops*-like larvae of three species of *Platygaster*; 26, second larval stage; 27, third larval stage. *a*, antenna; *ag*, salivary duct; *ao*, anus; *bsm*, ventral ectodermal thickening; *ed*, intestine; *ew*, rectum; *f*, furcal appendage; *fk*, fat-body; *ga*, genital organs; *gh*, proctodaeum; *gsae*, supra-oesophageal ganglion; *kf*, hook-like feet; *lfg*, lateral limbs; *lm*, *sp*, salivary glands; *md*, mandibles; *mo*, mouth; *msl*, stomach; *slk*, *slkf*, oesophagus; *tr*, tracheae; *ul*, lower lip.

lie as rudiments in a ventrally placed germ-band, and only attain development in the next stage. Into this latter the *Cyclops*-stage passes through a moult, and the larva is now an oval limbless body without segments (Fig. 182, 26). The nervous system, the salivary glands, and the proctodaeum now form as ectodermal invaginations, and the groups of muscles, by the arrangement of which the segmentation is recognisable, gradually develop. The last (third) larval stage, which follows the preceding after a moult, has the form of a segmented maggot devoid of limbs (27).

The larval forms in other related genera seem to vary greatly. In *Teleas* there is also a *Cyclops*-stage, but it is preceded by a spindle-shaped larva which is more equally segmented and has small stump-like mouth-parts, while still devoid of grasping hooks (Ayers). Development here begins with the formation of a coeloblastula (Metschnikoff, Ayers), in the inner cavity of which a lower layer forms by the immigration of cells. The rise of a median groove marks the bilateral symmetry of the embryo and an anterior thickening distinguishes the cephalic end.

All these larval forms of the *Pteromalidae* must be regarded as highly specialised, but we are not in a position to determine in individual cases the ontogenetic significance of the development of these remarkable forms.*

The larval forms of the Insecta are very varied. A comparative review of them shows most clearly that the manner of life of the larva is the chief factor in determining its outward appearance. We thus have, in the phytophagous larvae that feed on leaves, the eruciform type or polypod caterpillar, in the forms that bore into wood, a similar type with powerful mouth-parts and strong cephalic capsule, but with degenerate limbs; where the life of the larva is more or less parasitic, the form is that of a maggot, etc. In other groups (Orthoptera genuina), the larvae of which agree in their manner of life with the adult, the outward appearance of the imagines is to a large extent already found in the larval forms. It is evident from these considerations that the metamorphosis of the Insecta can only to a limited extent be utilised for phylogenetic purposes.

Above all, we must bear in mind that the larva which comes from the egg already shows the typical segmentation of the body, and that, therefore, in no single case are the ancestral forms which preceded the oldest Insect forms reproduced in the larvae. All that we can learn from the larvae of the Insecta is of value merely within the limits of this class.

* [Kulagin (No. XXVIII.) has recently reinvestigated the development of *Platygaster* with special regard to the origin of the germ-layers; there is no yolk, and the total cleavage which occurs is regarded by this author as a modification of superficial cleavage. Henneguy (No. XII.) similarly finds total cleavage and one embryonic envelope in the nearly allied *Chalcididae*. A curious condition is found by Marchal (No. XXXIII.) in *Encyrtus fuscicollis*, a form closely related to *Platygaster*; here the ovum gives rise, not to one egg, but to a legion of small morulae, which form chains of 50-100.—Ed.]

The absence of wings in all insect larvae points back to the primitive nature of the Thysanura, and many insect larvae actually agree closely in appearance with the members of this genus. The Campodeiform larvae, the importance of which was specially pointed out by BRAUER (No. 145), would thus represent the larval type which has most nearly retained the primitive character. As the chief characteristics of this type we would name: biting mouthparts, jointed antennae, thoracic segments more or less resembling the abdominal segments, well developed thoracic limbs, a long, slender, ventrally compressed form of body, and two jointed processes (cerci) at the end of the abdomen. This type is fairly accurately adhered to by the larvae of the *Ephemeridae*, *Perlidae*, many Neuroptera, and many Coleoptera.

The metamorphosis of the Insecta, as a rule, is more sharply marked in the higher orders, the separate stages being more unlike one another, and the transition between them not being gradual. We must therefore regard incomplete metamorphosis as the more primitive condition, and complete metamorphosis as a higher grade of individual development acquired in the Insecta. Consequently, the larvae of the Metabola must all be considered as derived forms. But in the Hemimetabola also, certain characters, phyletically considered, must also be regarded as new acquisitions, *e.g.*, the presence of a so-called closed tracheal system and of tracheal gills in many aquatic larvae, since, in all probability, this manner of life must be considered as only recently adopted.

While, therefore, little importance attaches, phyletically, to the larval forms of Insects, certain features are perhaps of some value, in so far as the acquired larval forms also show a tendency to reproduce the morphological characters of the ancestral forms. Among the features which have thus come to the surface again, we have: (1) the softer nature of the integument of the body-surface; (2) the less marked separation of the thorax from the abdomen; (3) the more uniform segmentation of the extremities; (4) the absence of the facet-eyes; (5) the frequent occurrence of abdominal limbs.

2. Development of the Imago.

We have already (p. 355) pointed out the characteristic distinction existing between the homomorphous orders of Insects on the one hand, and the holometabolic forms on the other with regard to the manner of development of the sexually mature (imaginal) condition. In the first group, the development of the adult is accomplished through a series of gradual internal and external changes, not differing essentially from the ontogenetic processes which occur in the metamorphosis of most other animals. We can here trace back the development of the wing-rudiments, the external genital apparatus, and all other alterations of form to simple growth of the larval body. The transformation of the internal organs, chief among which are the genital organs, is accomplished in an equally simple manner. We may perhaps assume, although this point has not yet been thoroughly investigated, that, simultaneously with the growth of the internal organs, a gradual regeneration takes place in them, as, indeed, is frequently the case with functional organs. We may assume that some of the cells or cell-groups, exhausted through the performance of their vital functions, are absorbed and replaced by fresh elements, so that a constant gradual regeneration of these organs is in progress.

In the holometabolic orders of Insects, on the contrary, the transition from the last larval stage to the adult form is accomplished through the intercalation of a resting stage (*pupal stage*), in which the acts of feeding, and usually also of locomotion, are suppressed, while the whole life-activities of the organism seem directed towards the important and complicated ontogenetic processes, which involve a complete destruction of many of the organs of the larva and their renewal from certain rudiments (*imaginal discs*) already present in the latter. Only a few of the organs found in the larva pass directly over into those of the pupa and the imago. Among these we must reckon the rudiments of the genital system. The heart also and the central part of the nervous system undergo only slight changes. Most of the other organs of the larva, on the contrary (the hypodermis, most of the muscles, the whole of the intestinal canal, and the salivary glands) are completely destroyed. Their cells, under the influence of the blood-corpuscles (leucocytes), which here act as phagocytes, break up into pieces which are taken in and digested by the latter, while, simultaneously with these processes of disintegration, the reconstruction of the organs from the formative centres (imaginal discs) already present in the embryo is accomplished in such a way as, in most cases, to preserve the continuity of the organ. We shall only be able to understand these processes by regarding them as an extreme case of the regenerative processes, which we assumed must occur in the Homomorpha. We shall then have to assume that at first only a part of the rudiment of an organ develops and functions for the use of the larva; this part becomes exhausted during larval life, so that it is no longer capable of performing its functions and therefore disintegrates, while another part of the rudiment remains from the first in an undeveloped condition, persisting as the imaginal disc, in order, during the pupal stage, to undertake the regeneration of the organ.

It should here be pointed out that this remarkable method of development of the organs of the imago, although most marked in the Insecta, is also found indicated in other animal groups. We find repeatedly that, instead of the gradual transformation of a larval organ into the corresponding adult organ, another course is entered upon, the larval organ being destroyed or degenerating, and the corresponding organ in the adult appearing anew as a rudiment. We refer here to Vol. ii., p. 312, where the disappearance and reappearance of limbs during the metamorphosis of the Crustacea is described. A similar phenomenon was mentioned in connection with the Acarina (pp. 104 and 105), in which a partial destruction and a reconstruction of the internal organs occurs. Where the distinction between the larval and the imaginal form of an organ is very marked, the latter mode of development may even appear as a simplification of the ontogenetic process.

Although SWAMMERDAM had already shown that the limb-rudiments can be recognised under the integument of the larvae of holometabolic insects, our more detailed knowledge of the changes connected with the pupal stage is due to the researches of WEISMANN (No. 129) in connection with the ontogeny of the Diptera. The fact that later students of this subject, among whom should be named GANIN, VIALLANES, KÜNCKEL D'HERCULAIS, KOWALEVSKY (No. 112), and VAN REES (No. 121), restricted their investigations to the same order, accounts for our being most familiar with the processes of metamorphosis in the pupa of the Dipteran family *Muscidae*. Our description will therefore chiefly refer to this family. But since, as is easily seen, we have in the *Muscidae* the most complicated and the most modified ontogenetic conditions, we shall often have to take as starting-points the simpler formative processes found in other Holometabola, such as the Nematocera (*Corethra*), the Hymenoptera, and the Lepidoptera (WEISMANN, GANIN, DEWITZ, etc.). It should be mentioned that our knowledge of the subject is still very incomplete, and only the principal features can be regarded as established. We have, especially, no knowledge as to how far the conditions of the inner metamorphosis ascertained as prevailing in the *Muscidae* occur also in the other groups of Insecta, although it must be regarded as probable that similar processes take place in the pupae of the Lepidoptera, Hymenoptera, and perhaps also of the Coleoptera.

We shall consider these ontogenetic processes under two heads, discussing first the development of the external form of the body, and then the rise of the internal organs of the imago.

A. Development of the external form of the Body.

The external form of the imaginal body is already complete in rudiment in the pupa, so that the passage of the pupa into the imago takes place merely by an unfolding and hardening of parts already present. The form of the body of the imago must therefore be prepared in the last larval stages, and attains complete development at the pupal moult (the transition to the pupal stage).

In most cases the transition from the larval shape to that of the imago consists principally of a modification of parts already present, new rudiments participating in it only to a limited extent. In the Lepidopteran caterpillar, for example, the head, together with the antennae and mouth-parts, and, further, the thoracic limbs (though in an essentially modified form) pass over direct from the larva to the pupa. The compound eyes and the wing-rudiments arise as new rudiments. The latter appear on the meso- and meta-thorax of the larva in the form of *imaginal discs* (*wing-discs*). The same is the case in very many other Holometabola, in which the transition from the larva to the pupa rests essentially upon a transformation of parts already present. We ought here further to mention modifications which occur in the abdomen, and which consist partly of the growth of the abdominal rudiments (extremities?) into external genital organs (ovipositors, poisonous stings, pp. 299 and 300), and partly of an apparent diminution in the number of segments. The latter may be brought about by a fusion of distinct segments, or by a union of the first abdominal segment with the meta-thorax (Hymenoptera), or else may be traced to a transformation of the most posterior segments into a telescopic genital appendage (ovipositor, penis).

In those cases in which the larva is limbless (Diptera, many Hymenoptera, and Coleoptera), the limbs of the imago also arise as new formations in the form of imaginal discs (limb-discs).

The metamorphosis of *Corethra* (Weismann, No. 130) may serve as an example of the simpler type of metamorphosis. The larva belongs to the eucephalic type of Dipteran larvae, and consequently the head of the adult is present as a rudiment in this stage; this larval head, through certain modifications of its parts, passes directly over into the pupa. Even the compound eye is already found in the larva, a rare and exceptional occurrence among the Holometabola. The thoracic limbs, the wings and the halteres, on the contrary, are developed as entirely new rudiments. We consequently find, in the last larval stage that precedes the pupal stage, correspondingly arranged *imaginal discs.* Each thoracic segment shows four such discs, two ventral and two dorsal (Fig. 183, *ba* and *fa*). The ventral discs (*ba*) become the limb-rudiments. Of the dorsal pairs of discs (*fa*), that occurring in the meso-thorax becomes changed into wings, that in the meta-thorax into the halteres, while the corresponding rudiment in the pro-thorax yields, in *Corethra*, the stigma-bearing dorsal process and, in *Simulia*, a tuft of tracheal gills. If we examine such a rudiment (imaginal disc) of a limb more closely, we see that the limb itself as elsewhere (*e.g.*, in the Hemimetabola) arises as an outgrowth of the surface of the body. The only distinction here found is that the limb-rudiment, as a whole, appears sunk below the level of the surface of the body. It arises at the base of an invagination, in the same way as the head- and trunk-discs in the *Pilidium* larva of the Nemertini (Vol. i, p. 221), and the rudiment of the lower surface of the Echinoid body in the *Pluteus* (Vol. i., p. 439). Such instances of the occurrence of rudiments of important parts of the adult body in an invaginated condition might easily be multiplied. For instance, the body-wall of the primary zooecium of the ectoproctous Bryozoa is found invaginated in the larva (as the sucking-disc and mantle-cavity). The lumen of the invagination in which the limbs of *Corethra* (and of other Holometabola) appear as rudiments was called by **Van Rees** the *peripodal cavity*, and the sheath which bounds it externally, and which naturally is continuous with the hypodermis, was named the *peripodal membrane.*

Fig. 183.—Diagrammatic transverse section through a thoracic segment of a larva of *Corethra* (from Lang's *Text-book*). *ba*, limb-rudiment; *fa*, wing-rudiment; *be* and *fe*, peripodal depressions; *lhy*, larval hypodermis; *lh*, chitinous cuticle of the larva.

We must assume that, from the very first, an ectodermal and a mesodermal portion derived from the corresponding layers of the germ-band, take part in the rudiments of the limbs. The ectoderm of these rudiments is in continuous connection with the peripodal membrane, and through it with the hypodermis covering the larval body. **Weismann** was inclined to derive the organs that develop within the limb-rudiments (tracheae, muscles, etc.) from growths of the neurilemma of a nerve joining the imaginal disc. For nerves and tracheal ramifications appear early on the inner surface of the imaginal discs.

When the limb-rudiments increase in size, the peripodal membrane is correspondingly stretched, while the appendage within it assumes a more or less bent position. In consequence of this, the wing-rudiments seem folded, and the rudiments of the legs in *Corethra* are spirally coiled. The unfolding of the limb-rudiments is brought about by their protrusion from the invagination in which they were at first hidden. As they become more and more protruded, the peripodal depression becomes continually shallower, and finally the peripodal membrane becomes completely evaginated and forms a part of the general hypodermis.

The internal organs of *Corethra*, as compared with those of other Holometabola, seem during metamorphosis to undergo only unimportant alterations. Of the striking processes of disintegration and of subsequent regeneration, which have been so well established for the *Muscidae*, nothing is to be observed in *Corethra*. It deserves to be mentioned, however, that, according to KOWALEVSKY (No. 112), a disintegration of the larval and the development of the imaginal epithelium of the enteron of *Corethra* takes place in the same way as in *Musca* (see below, p. 383). Most of the larval organs pass directly over into the pupal and imaginal stages; the general musculature also remains unaltered, but the muscles of the limbs and of the wings come from new rudiments. The latter, according to WEISMANN, arise in the last larval stage from cell-strands which appeared as rudiments in the embryo.

When we consider the unimportant character of the internal changes which occur during the metamorphosis of the *Tipulidae*, of which *Corethra* serves as an example, we shall hardly doubt that the conditions here found represent a transition from the incomplete to the complete method of metamorphosis. This is confirmed *inter alia* by the short duration of the pupal stage and its capacity for free movement, as also by the early appearance of the compound eye, a character which *Corethra* has in common with the Hemimetabola.

We must now describe more in detail the development of the wings, which has been best ascertained in the Lepidoptera by SEMPER (No. 126), LANDOIS (No. 114), PANKRITIUS (No. 120), and SCHÄFFER (No. 124a). The wings, like the other rudiments of extremities, arise as simple outgrowths of the hypodermis within a peripodal depression. They thus at first represent a simple fold of the hypodermis, the point of insertion of this fold being connected internally with peculiar modifications of the fat-body and of the tracheal system. The fat-body at this point shows accumulations of small cells, which have been regarded by SCHÄFFER as formative centres. The tracheae which join the wing-rudiments form a close network of very fine tracheal tubes, which develop as intracellular structures within single large matrix-cells (LANDOIS, SCHÄFFER). These networks of tracheae degenerate *after the pupal stage has been entered upon*. On the other hand, large tracheal ramifications develop which run into the wings and lead to the development of their venation. When the caterpillar passes into the pupa, the wing-rudiments are evaginated from the peripodal cavity by the action of increased blood-pressure. The wing-rudiments thus become vesicles filled with blood which contain tracheal ramifications. At a later stage, however, the layers corresponding to the future upper and lower surfaces of the wings become closely applied and fuse, except along those lines that are occupied by the tracheal ramifications; here also the blood-fluid circulates, and these lines become transformed later into the network of veins in the wing. In later stages, tracheae are no longer to be found within the veins; they have either degenerated or, as in *Musca*, according to WEISMANN, they have been withdrawn out of the veins into the thorax. There, however, remains in the veins a strand, which was discovered by SEMPER in the Lepidoptera, and which in early stages accompanies the tracheae; this we may call the *rib-strand* (SEMPER'S *wing-ribs*). It resembles a tracheal tube, and consists of an outer matrix and an inner intima which gives off projecting dendriform processes into the lumen. The centre of the lumen is occupied by a longitudinally striated strand (a secretion ?). SEMPER was able to prove the connection of these rib-strands, which, in the adult, are only to be found in the basal half of the wing, which they serve to support, with the tracheal system. These strands must therefore be transformed tracheae. Nerve-trunks are also found in the wing-veins.

The cuticle of the wing, which does not develop until somewhat late, is considerably thickened on the surface of the veins. The manner in which the two hypodermal lamellae of the wings fuse is of some interest. A "basal membrane" develops on the inner surface of the hypodermis on each side, while the hypodermal cells themselves become pillar-like. The two basal membranes become closely applied to one another, fuse, and finally disintegrate, so that, in the adult wing, the hypodermal pillars extend continuously throughout the whole thickness of the wing.

It should here be mentioned that the facts of ontogeny are not favourable to ADOLPH'S theory of wing-venation. According to this theory, the veins of the fully formed wing are to be divided into convex and concave veins, which differ in their origin, the concave veins being derived from tracheae, while the convex veins develop out of cell-strands into which tracheae can extend only secondarily. The system of convex veins and that of concave veins are originally altogether distinct. But it has been proved by BRAUER and REDTENBACHER (No. 101) for the wings of the Odonata, and by GRASSI for those of the Termites, and more recently by HAASE (No. 108) for those of the Lepidoptera, that the branches of one and the same tracheal trunk may be changed partly into convex and partly into concave veins, so that the postulate on which the theory rests is negatived. This theory is also opposed by VAN BEMMELEN (No. 99), who confirms the observation made by FR. MÜLLER in connection with the *Nymphalidae*, that the system of veins in the Lepidoptera immediately after entering the pupal stage differs in details from that of the adult form. The observation of the development of the venation in the wings has thus a certain phylogenetic significance.

The hairs and scales of the Lepidopteran wing arise as outgrowths of single hypodermis-cells (mother-cells of hairs and scales, SEMPER). The characteristic definitive markings develop only after the differentiation of the scales. It must, however, be mentioned that, according to VAN BEMMELEN, the permanent markings are preceded by transitory markings, which are essentially distinct from the former, but have a few features in common with them.

Much more complicated ontogenetic processes are met with in the *Muscidae*. The limb- and wing-rudiments here arise in the same way as in *Corethra*. But, in the *Muscidae*, the whole of the imaginal rudiment is shifted much further into the interior of the body, the peripodal cavity appears closed and the peripodal membrane is connected with the hypodermis merely by a delicate thread-like stalk (Fig. 184 *A*, *is*; Fig. 185 *A*, *st*). These connective stalks, which were recognised by **Dewitz*** (No. 102), who correctly grasped their significance, have a fine lumen, as was shown by **Van Rees** (No. 121), who has recently studied these structures more closely. Although the first development of the imaginal discs in the embryo of the *Muscidae* is still unknown, we shall not err in tracing them back, like those of *Corethra*, to hypodermal invaginations. We must then regard the stalk-like connection as the long drawn out neck of this invagination.

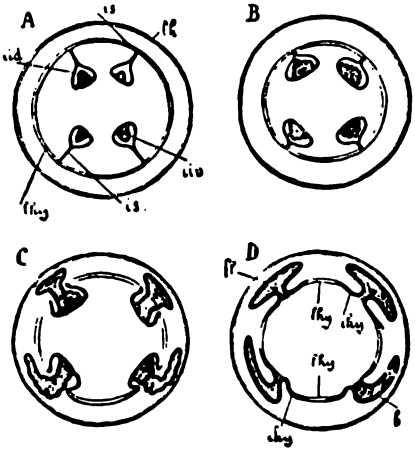

FIG. 184.—Diagrammatic transverse section through the larva and pupa of *Musca*, to illustrate the development of the wings, the legs, and the imaginal hypodermis (from LANG's *Text-book*). *b*, limb-rudiments; *fl*, wing-rudiments; *ihy*, imaginal hypodermis, in *D* extending from the base of the imaginal discs; *iid*, imaginal discs of the wings; *ifr*, imaginal discs of the legs; *is*, strand connecting the rudiment with the hypodermis; *lh*, chitinous integument of the larva; *lhy*, larval hypodermis (indicated by two thin parallel outlines, while the imaginal hypodermis is represented by thick black lines).

In other respects the development of the extremities (Fig. 184) takes just the same course as in *Corethra*. The rudiments of the legs increase in size and early show traces of the later segmentation. They appear packed into the peripodal cavity in such a way that the different joints of the limbs telescope into each other "like the rings of a traveller's drinking cup" (as **Van Rees** appropriately expresses it). The evagination of the developed limb-rudiments, which occurs on the first day after the commencement of the pupal condition, takes place by the shortening of the stalk of the imaginal disc (Figs. 184 *B*, and 185 *B*) and the widening of its lumen, which allows the extremity, as in *Corethra*, to emerge finally through the widening aperture of the peripodal invagination (Figs. 184 *C*, and 186 *A*). While the latter at the same time gradually disappears, the peripodial membrane is utilised

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* **Künckel d'Herculais** (No. 113) also recognised these strands.

for the formation of a hypodermal thickening in proximity to the point of insertion of the limb, and this thickened part of the hypodermis gives rise, as we shall see below (p. 379), to the formation of the whole imaginal thorax, while the hypodermis of the larva disintegrates.

We must here touch upon the question of the first appearance of the mesodermal portion of the rudiments of the extremities. In the imaginal discs of developing larvae of *Musca*, a separation into an outer ectodermal and an inner mesodermal portion is always found. GANIN (No. 107) derives the mesodermal portion from a differentiation and delamination of the innermost layers of the ectodermal portion, and VAN REES has supported this view. KOWALEVSKY (No. 107), on the contrary, tends to the view that the mesodermal part of the imaginal discs is to be derived from the cells of the embryonic mesoderm. He finds, scattered in the mesoderm, beneath the hypodermis of the larva, so-called *wandering cells* (Fig. 190 *A*, *w*, p. 383), which differ in appearance from the leucocytes, and which represent the elements from which the formation of the mesodermal part of the imaginal rudiments proceeds. KOWALEVSKY is disposed to assume an imaginal rudiment for every segment, this rudiment being, however, so delicate and undifferentiated as not to be discoverable in the first stages. From these imaginal rudiments of the mesoderm, the above-mentioned wandering cells would be derived, and would only secondarily become connected with the imaginal discs.

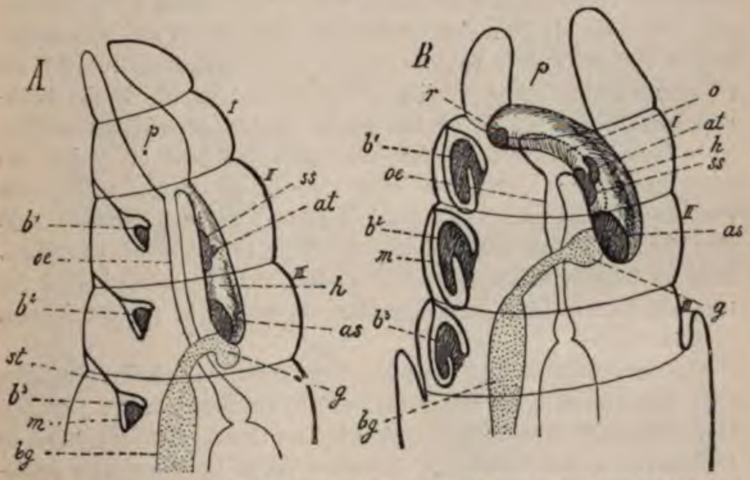

FIG. 185.—Diagrams illustrating the position of the imaginal discs in the larva (*A*) and pupa (*B*) of *Musca* (taken from VAN REES). The wing-rudiments are omitted. *as*, optic disc; *at*, antennal rudiment; b^1, b^2, b^3, rudiments of the three thoracic limbs; *bg*, ventral chain of ganglia; *g*, brain; *h*, so-called "brain-appendage"; *m*, peripodal membrane; *o*, aperture of the brain-appendage into the pharynx; *oe*, oesophagus; *p*, so-called "pharynx"; *r*, rudiment of the proboscis; *ss*, frontal disc; *st*, stalk-like connection between the peripodal membrane and the hypodermis; *I*, *II*, *III*, the three thoracic segments.

The development of the cephalic region in the *Muscidae* is more complicated, and still, in spite of the descriptions of **Weismann** (No. 129), **Van Rees** (No. 121), and **Kowalevsky** (No. 112), difficult to understand. In this connection we must recall the fact that the cephalic region, in the larva of the *Muscidae*, occurs in an extremely reduced condition, the head-region being represented only by the most anterior and smallest of the twelve segments of which the body of the conical larva is composed. Its small size is partly to be ascribed to the fact that a considerable portion of the head is here present in an invaginated condition. For, as has been shown by the researches of **Weismann**, the anterior part of the head, the mandibles, and the whole of the region surrounding the mouth are invaginated in the last embryonic stages, and in the fully-formed maggot are represented by that depression (Fig. 185, *p*) in which the hook-apparatus, characteristic of the larvae of the *Muscidae*, develops. This invaginated part of the head into the base of which the oesophagus now opens, has been named, not very happily, the *oesophageal bulb* or *pharynx*, and it must for the present be held that the cavity thus named does not belong to the alimentary canal. It is an invaginated section of the head, and the formation of the imaginal head consists for the greater part merely in the evagination of this region.

The first rudiments of the most important parts of the head (the eyes, the antennae, and the frontal region) are found in the youngest larvae as a pair of cell-masses lying in the thorax, closely applied to the halves of the brain (and therefore called by **Weismann** *brain-appendages*). These are, probably from their first origin, connected anteriorly with the pharynx, and might be described as the imaginal discs of the head. In the later stages these assume the form of a pair of long sacs expanding posteriorly (Fig. 185 *A* and *B*, *h*), and may no doubt, according to their origin, be regarded as outgrowths of the larval pharynx (see above). Epithelial thickenings soon appear in the walls of these sac-like "brain-appendages," and in these can be recognised the rudiments of definite parts of the head. A disc-like thickening appears in the posterior widened portion of each of the appendages, this represents the rudiment of the compound eye, and is consequently called the *optic disc* (*as*). On the basal surface of the optic disc there is a cellular expansion connected with the supra-oesophageal ganglion by a nerve. This nerve becomes the optic nerve of the adult, while the optic ganglion becomes more distinctly separated from the brain. In the anterior, more cylindrical or tubular portion of the "brain appendages" we find the *frontal disc* (*ss*), from which the antennal rudiment soon grows out in just the same way as do the limb-rudiments from the base of the imaginal disc that gives origin to them.

Originally (Fig. 185 *A*) the "brain appendages" lie somewhat far back, in the thorax of the larva, so that they connect the posterior part of the wall of the pharynx with the most anterior segment of the brain. Later, however, after the pupal stage has been entered upon, they, together with the central nervous system, shift further forward (Fig. 185 *B*), so that their anterior extremities, which are now bent ventrally, embrace the pharynx laterally (if we have rightly understood the descriptions of Weismann and Van Rees). At the same time the communication between the "brain-appendages" and the pharynx (Fig. 185 *B*, *o*) becomes wider and wider, and soon extends in the form of lateral oesophageal slits along the whole length of the brain-appendages. By this means, the lumina of the brain-appendages and of the pharynx flow together so completely that the two soon represent only one single vesicle, the *cephalic vesicle* (Fig. 186, *k*). The walls of the cephalic vesicle are nothing

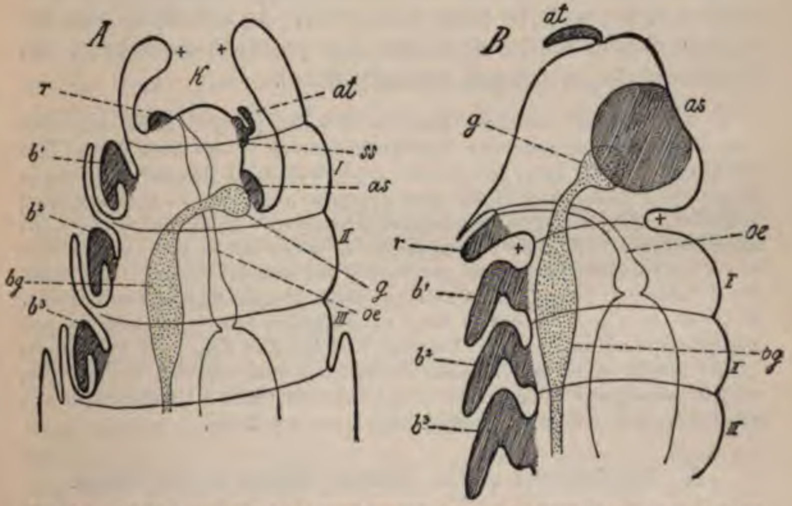

Fig. 186.—Diagram illustrating the transformations that take place in the pupa of *Musca* before it hatches (adapted from Kowalevsky and Van Rees). The wing-rudiments are not drawn. *as*, optic disc; *at*, antennal rudiment; b^1, b^2, b^3, rudiments of the three thoracic limbs; *bg*, ventral chain of ganglia; *g*, brain; *k*, cephalic vesicle (formed by the union of the pharynx with the brain appendage); *oe*, oesophagus; *r*, rudiment of proboscis; *ss*, frontal disc; *I*, *II*, *III*, the three thoracic segments.

more than the external surface of the permanent head, and the most important parts of the latter (antennae, eyes, rudiments of the proboscis) can already be recognised on them. It only remains for the cephalic vesicle to be evaginated through the aperture of the pharynx (+ to +), so as to produce the completed head of the pupa. By this evagination of the parts formerly invaginated, that which was before the aperture of the pharynx becomes the neck-region (Fig. 186 *B*, + to +), which now connects the head with the thorax (VAN REES). The protrusion of the "cephalic vesicle," which was directly observed by WEISMANN, seems to be caused by the increase of pressure from within, brought about by the contraction of the posterior parts of the body. In accordance with the conformation of the imaginal head thus produced, the anterior end of the oesophagus becomes ventrally flexed.

We have pointed out above that the so-called pharynx is nothing more than an invaginated portion of the external surface of the larval head. The "brain-appendages" must be regarded as diverticula of this invagination, in which the separate parts of the head appear as rudiments in an invaginated condition. They may thus be compared throughout with the rudiments of the thoracic limbs. All these "imaginal discs," according to their origin, have to be derived from invaginated portions of the external surface of the body. It is difficult to reconcile with this hypothesis the accounts of GRABER (No. 28), who in a later embryonic stage of *Calliphora* (*Musca* of most authors) observed the rudiments of the imaginal discs lying as simple epithelial plates in the interior of the body. Since GRABER left uninvestigated the preceding and the subsequent ontogenetic stages, we can only record his statement, and must leave the problem to be solved by future researches.

B. Development of the Internal Organs of the Imago.

It has already been mentioned that most of the organs of the larvae of the *Muscidae* (and of most Diptera, Lepidoptera, Coleoptera, and Hymenoptera) undergo disintegration through the action of the blood-corpuscles (leucocytes), and that their reconstruction proceeds from certain embryonic cell-groups, the imaginal discs. Disintegration and reconstruction take place during the pupal stage so gradually that in many cases the continuity of the organ is not disturbed

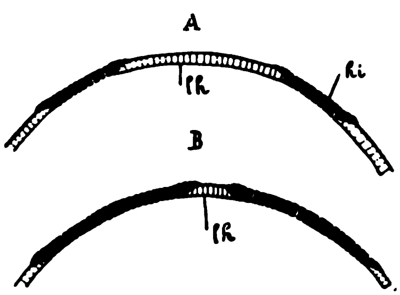

FIG. 187.—Diagram illustrating the formation of the imaginal hypodermis in the abdomen of the *Muscidae* (from LANG's *Text-book*). *hi*, imaginal discs of the hypodermis; *lh*, larval hypodermis.

during the course of these processes. Such transformation affects especially the hypodermis, the intestinal canal, the muscles, the fat-body, and the salivary glands. The modification of the tracheal system can only to some extent be classed in this category; otherwise it appears to be due to simple regeneration through division of the cells. The heart, the central nervous system, and the genital rudiments undergo slighter alteration. The changes that take place in the different organs must now be discussed separately.

Hypodermis.

The hypodermis of the imago arises through an extension of the ectodermal portion of the imaginal discs. This has already been stated in connection with the thorax (p. 375). While the limbs of the thorax gradually attain development in the pupa, a hypodermal layer, consisting of numerous small cells, extends from their points of insertion; this layer, which apparently arises from the peripodal membrane, spreads more and more over the surface of the pupal thorax, while at the same time the area of the large-celled larval hypodermis is correspondingly more and more circumscribed. The flat edges of the newly-formed hypodermis (Figs. 187, *hi* and 188, *i*) grow into the slit between the superficial cuticle and the larval hypodermis (Fig. 188, *h*), so that, at these points, the old hypodermis which is undergoing disintegration comes to lie on the inner side of the newly-formed epithelial layer (Fig. 188 *B*). It is thus evident that, during the substitution of the new for the old hypodermis, the continuity of the superficial epithelium does not anywhere appear interrupted. Since the edges of these two hypodermal envelopes overlap, there is not anywhere a point of the body-surface devoid of epithelium. The disintegration of the larval hypodermis is accomplished by the action of the leucocytes (Fig. 188, *k*), which become massed in the neighbourhood of the disintegrating hypodermal cells and ingest the latter. Since the assimilated fragments assume the shape of rounded granules, the leucocytes may now be distinguished by the name of the *granular spheres* (WEISMANN). The granular spheres, which abound in the future body-cavity of the pupal stage, are therefore nothing more than leucocytes (blood-corpuscles) which have assimilated the disorganised tissue of the disintegrating larval body. It should here be noted that the breaking-up of the larval tissues is not preceded by the death of the cells, but is the result of the action of leucocytes on the still living tissues which have lost their active functions. While tissues fully capable of vital activity, *e.g.*, those of the imaginal discs, resist the attack of the leucocytes, the larval tissues, less capable of vital activity, are broken up into fragments by the attack of the leucocytes, and are simply devoured and digested by them. These processes may best be followed in the disintegration of the larval musculature. The destruction of most larval organs is thus due to the capacity for the taking in of nourishment and for intracellular digestion possessed by the amoeboid blood-corpuscles. This capacity has been specially emphasised by METSCHNIKOFF (Nos. 116 and 117), who with reference to this significance of the blood-corpuscles has called them *phagocytes*.

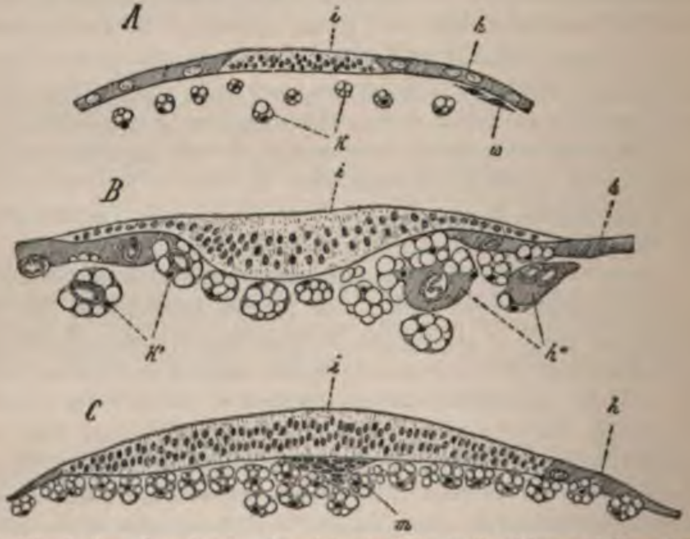

FIG. 188.—Sections through a hypodermal imaginal disc in the abdomen of *Musca* (after KOWALEVSKY). *A*, through the larva. *B* and *C*, through the pupa. *h*, larval hypodermis; *h'*, detached portions of the same attacked by phagocytes; *i*, imaginal disc; *k*, phagocytes containing disorganised hypodermal cells (so-called granular cells); *k'*, phagocytes enclosing hypodermal nuclei; *m*, mesodermal rudiment of the imaginal disc; *w*, wandering cells.

The re-formation of the hypodermis is accomplished in the head and in the abdomen in the same way as in the thorax. In each of the eight segments of which the abdomen of the larva consists, there are, according to GANIN (No. 107), four islands of small cells; these are the imaginal discs (Figs. 187, *hi*, and 188, *i*) from which the re-formation of the hypodermis proceeds. VAN REES has recently discovered another pair of small imaginal discs on the abdominal segments. The four discs that occur on the last body-segment, closely crowded together, encircle the anal aperture (Fig. 189, *ims*) and take part in the formation of the proctodaeum, yielding the rudiments of the rectal sac and the rectal papillae. To this segment apparently also belong the two pairs of imaginal genital rudiments (rudiments of the external genital organs) which were demonstrated by KÜNCKEL D'HERCULAIS (No. 113) in *Volucella.*

It should be mentioned that a cell-accumulation representing the permanent mesoderm (Fig. 188 *C*, *m*) is found on the inner surface of the abdominal imaginal discs as on that of the thoracic discs, this accumulation being the starting-point for the development of the mesodermal structures of the abdomen. KOWALEVSKY, as above mentioned (p. 375), has traced back the origin of this mesoderm-accumulation to the so-called wandering cells (Fig. 188 *A*, *w*), while earlier authors were inclined to derive them through delamination from the ectoderm of the imaginal discs.

The newly-formed hypodermis extends very rapidly over the surface of the body, so that the areas of hypodermis originating from the different imaginal discs soon flow together. While this perfecting of the permanent hypodermis is taking place, that of the larva is finally destroyed by the phagocytes.

Musculature.

The greater part (or the whole mass) of the larval musculature undergoes a process of disintegration by means of phagocytes precisely like that described above in connection with the larval hypodermis; the disintegration of the muscles is, indeed, the first process to take place in the pupa. The muscles of the most anterior segments of the body disintegrate first; and the superficial layers are affected before the deeper ones.

The disintegration of the larval muscles is brought about in the following way. A large number of amoeboid blood-corpuscles, which have collected on the surface of the muscle-bundle, penetrate through the sarcolemma and wander into the interior of the muscle-substance, pressing into fissures which develop in it. It often appears as if the muscle-substance is actually cut out in the parts corresponding to the processes of the phagocytes which extend into it. The muscle, in this way, breaks up into a number of particles which soon become rounded and are immediately swallowed by the phagocytes. The muscles are thus transformed into a great accumulation of granular spheres, which finally shift apart and become scattered in the body-cavity of the pupa. The muscle-nuclei are digested and assimilated by the phagocytes in the same way as the muscle-substance.

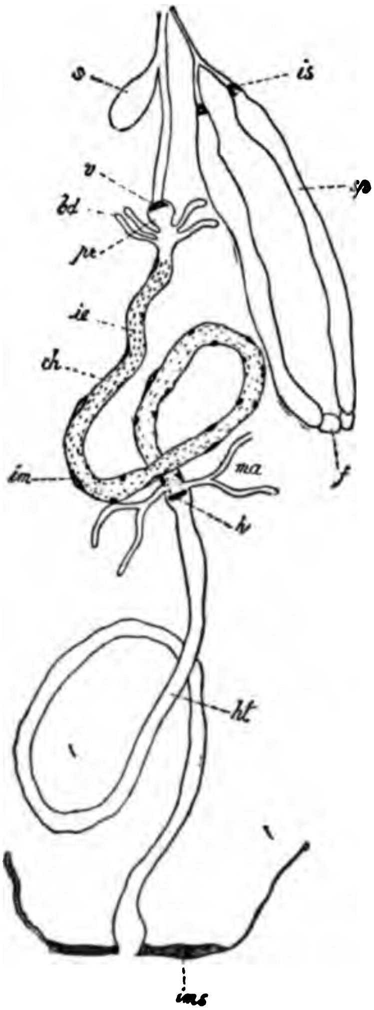

Fig. 189.—Larval digestive tract of one of the *Muscidae* with the imaginal discs depicted (after Kowalevsky). *bd*, caecal tubes of the chylific stomach; *ch*, chylific stomach; *f*, fat-cells at the apex of the salivary glands; *h*, proctodaeal imaginal ring; *ht*, proctodaeum; *ie*, imaginal cells of the mid-gut epithelium; *im*, imaginal cells of the muscles of the mid-gut; *ims*, posterior abdominal imaginal disc; *is*, imaginal rings of the salivary glands; *ma*, Malpighian vessel; *pv*, proventriculus; *s*, sucking stomach; *sp*, salivary glands; r, stomodaeal imaginal ring.

Van Rees and Kowalevsky are in entire agreement with regard to the details of the disintegration of the larval muscles by phagocytes, which had already been the subject of conjecture to Metschnikoff and Ganin. According to Van Rees, not all the muscles of the larva undergo such disintegration. Certain dorsal groups of the external oblique muscle of the second thoracic segment are retained and pass over into the wing-muscles of the adult after radical internal modifications consisting of an increase in the number of the nuclei and a rearrangement of the muscle-substance. This manner of transition from larval to imaginal musculature appears very remarkable, but the descriptions of Van Rees leave hardly any doubt as to the accuracy of these observations.*

As a rule, the formation of the imaginal muscle-groups takes place from the permanent mesoderm, which is derived from that of the imaginal discs (Fig. 188 *C*, *m*). We have already stated (pp. 375–381) all that is as yet known as to the origin of the former.

Intestinal Canal.

The disintegration of the larval intestine and the development of the permanent

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* [According to recent investigations by Kawawaiew (No. XXIV.), phagocytosis plays a very unimportant rôle in the metamorphosis of *Lasius*, this being especially noticeable in the disintegration of the larval muscles; the phagocytes here do not cause the liquefaction of the fibres, but are only concerned in the absorption of the liquid mass.—Ed.]

organ from distinct imaginal discs take place, as with the hypodermis, side by side, in such a way that the continuity is not anywhere interrupted. We owe our knowledge of the imaginal discs of the intestinal canal to **Ganin** (No. 107). More recently, **Kowalevsky** (No. 112) and **Van Rees** (No. 121) have described the development of the intestinal canal in detail.

The imaginal discs of the intestine, which in the pupa is very short, are found in the enteron in the form of numerous scattered cell-islands (Fig. 189, *ie*); in both the stomodaeum and proctodaeum these appear as a ring (*v* and *h*) of imaginal tissue capable of great increase. The imaginal ring of the fore-gut (*v*) lies in the region of the so-called proventriculus (*pr*, cf. Fig. 191, *im*), while that of the hind-gut is to be sought immediately below the aperture of the Malpighian vessels. The regeneration of these two parts of the intestinal canal is not exclusively brought about by these two rings, but the imaginal rudiments of the neighbouring parts of the body-surface participate in it. It thus appears that the most anterior part of the oesophagus is yielded by the imaginal discs round the mouth, while the discs of the eighth abdominal segment that surround the anus (Fig. 189, *ims*) produce, by invaginating, the rectal sac and the rectal papillae.

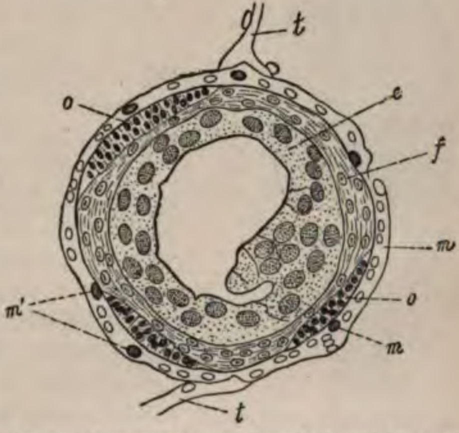

Fig. 190.—Transverse section through the pupal mid-gut of one of the *Muscidae* (after **Kowalevsky**). *e*, degenerating larval epithelium; *f*, the newly-formed cell-layer round the same; *m*, muscular coat; *m'*, imaginal cells of the muscular coat; *o*, imaginal discs of the mid-gut epithelium; *t*, tracheal trunks.

The development of the permanent mid-gut (chylific stomach) proceeds in such a way that the island-like imaginal discs, increasing considerably in number, extend over the external or basal surface of the epithelium of the larval enteron (Fig. 190, *o*) until they come into contact and fuse, the wall of the imaginal intestine being thus formed. The whole of the larval enteric epithelium (*e*) is at the same time cast off into the interior of the gut and, surrounded by a layer of small cells (*f*), perhaps derived from the imaginal discs, as well as by a gelatinous envelope, forms the so-called yellow body which, until its disintegration, remains lying in the pupal intestine. The larval muscular coat (*lm*) remains intact so long as the imaginal mid-gut is not completely developed, but is afterwards attacked by phagocytes and destroyed. The permanent muscular layer develops from single cells lying on the outer surface of the imaginal discs (Figs. 189, *im* and 190, *m*), which must be described as special imaginal cells of the intestinal muscles.

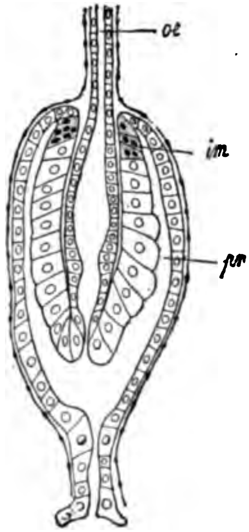

Fig. 191.—Longitudinal section through the larval proventriculus of one of the *Muscidae* (after Kowalevsky). *im*, stomodaeal imaginal ring; *oe*, oesophagus; *pr*, proventriculus.

The metamorphosis of the fore-gut is commenced by the degeneration of the proventriculus and of the sucking stomach. The proventriculus or gizzard (Fig. 191, *pr*), which seems to be formed by a process of infolding or intussusception of the fore-gut, degenerates through the flattening out of this fold. The sucking stomach also degenerates in a similar way, retreating more and more into the oesophagus, so that, in place of the original diverticulum, there now only remains a widening of the lumen of the oesophagus. At the same time, this part of the gut is attacked and disintegrated by phagocytes, while the disorganised parts are replaced by the gradually extending imaginal portions of the wall. The imaginal ring of the fore-gut (Fig. 191, *im*), which, according to Kowalevsky, undertakes the formation of a great part of the permanent oesophagus, closes posteriorly, so that the communication with the mid-gut seems to be interrupted.

The transformation of the hind-gut takes place in a similar manner. Here also the imaginal ring extends so as to form a tube which, growing round the opening of the Malpighian vessels, closes towards the mid-gut, while posteriorly it is connected with the disintegrating proctodaeum. In a similar way, the territory of the proctodaeum is circumscribed by an imaginal tube growing from behind, formed by one of the imaginal discs found in the neighbourhood of the anal aperture, till finally, when the whole of the larval hind-gut is changed into granular cells, the two imaginal sections of the tube seem to be approximated until they come into contact.

In the above description, we have mainly followed the accounts of KOWALEVSKY. According to VAN REES, the reconstruction of the fore- and hind-guts is brought about, not merely by the imaginal discs already mentioned, but a simultaneous regeneration of the larval epithelium takes place, only some of the cells of the larval epithelium undergoing disintegration, while others, on the contrary, undergo repeated division and form a portion of the imaginal oesophagus.

The salivary glands of the larva (Fig. 189, *sp*) are entirely destroyed by phagocytes. They are reconstructed from the imaginal discs which, according to KOWALEVSKY, form a ring at the anterior end of the glandular tube (*cf.* the statements of SCHIEMENZ, No. 125).

From the accounts hitherto given, it is difficult to make out what kind of transformation is undergone by the Malpighian vessels. According to VAN REES, a regeneration of the larval cells through division may take place, or these elements may disintegrate.

The method of transformation of the intestinal canal described above seems very widespread among the holometabolic Insecta. It has been observed not only in Diptera, but also in Lepidoptera (KOWALEVSKY, FRENZEL), Coleoptera (GANIN), and Hymenoptera (GANIN). The casting of the mid-gut epithelium was also found by KOWALEVSKY in *Corethra*, *Culex*, and *Chironomus*.

[In this connection the more recent works of RENGEL (No. XXXVII.), MÖBUSZ (No. XXXIV.), and KARAWAIEW (No. XXIV.) should be consulted.—ED.]

The Tracheal System.

The fact that the tracheal system undergoes important transformation during metamorphosis is demonstrated by the entirely different form assumed by it in the larva, the pupa, and the imago. We have only to recall that the larva of the *Muscidae* breathe through a pair of stigmata at the posterior end of the body, the pupa through one occurring in the pro-thorax, while the imago possesses six pairs of stigmata (situated on the meso-thorax, meta-thorax, and four abdominal segments). There is no doubt that in the larva and pupa the other stigmata are closed. The tracheal strands connected with the latter, as well as some other parts of the tracheal system, as pointed out by WEISMANN, seem to function as imaginal discs for the regeneration of the tracheal matrix (VAN REES), and a regeneration of this epithelium can also frequently be seen to proceed from simple division of the cells. The disintegration of the degenerating parts of the tracheal system is accomplished under the influence of phagocytes in the way already described.

The Nervous System.

The central parts of the nervous system pass directly over from the larva to the imago, although they undergo considerable modifications of form and position. At the same time certain histological changes, known as *histolysis*, are said by **Weismann** to take place in them, *e.g.*, a disintegration and reconstruction of the tissues within the organs without disturbing their continuity. Recently, however, the term hystolysis has been applied to the disintegration of the tissues of the pupa generally.

We have as yet little light on the question of the transformation of the peripheral nervous system. Although it must be considered probable that the destruction of the larval muscles is accompanied to some extent by a degeneration of the motor nerves, this is not the case with the nerves that run to the extremities. These can be recognised in the larva in the form of nerve-strands connecting the imaginal discs with the central nervous system. These strands, according to **Van Rees**, pass over from the larva to the pupa and imago, so that, when the limb-rudiments develop further, only the distal parts of the nerves belonging to them appear as new formations.

The Fat-body.

The fat-body of the larva also is destroyed through the action of the phagocytes in the way described in connection with other tissues. Its reconstruction appears to proceed from the mesoderm of the imaginal discs. It is possible also that the accumulations of embryonic cells, assumed by **Schäffer** to be formative centres, have to do with the regeneration of the fat-body. In any case it is to be derived from mesodermal tissue. Even though **Wielowiejsky** observed the origin of the fat-body in *Corethra* from a cell-layer lying beneath the hypodermis of the larva, such an observation does not necessarily support the view of **Schäffer**, who thought he had convinced himself that, in *Musca*, the fat-body of the larva is derived partly from the hypodermis and partly from the tracheal matrix, and thus from ectodermal tissue.

The ultimate fate of the Phagocytes.

We have seen that the development of the imaginal organs, in cases where these are not taken over direct into the pupa, always proceeded from the imaginal discs. The phagocytes, the number of which increases greatly in the pupa, do not (as was formerly thought) take any direct share in the building up of the tissue. Their significance seems to be that of destroyers of the larval organs which are doomed to destruction; the constituent parts of these organs are taken in and digested by them, and, through their capacity of locomotion, they conduct particles of nourishment to the organs that are in process of reconstruction. But what is the fate of these elements after the ontogenetic processes in the pupa are completed? There can be no doubt that some of the so-called granular cells develop into ordinary blood-corpuscles. The majority of them apparently undergo degeneration. The phagocytes themselves are finally used as food for the newly-formed tissues. Interest attaches here to the observation of VAN REES that many phagocytes finally wander into the newly-formed hypodermis, and there, in the spaces between the hypodermal cells, undergo degeneration.

General considerations regarding the development of the Imago in the Pupa.

We have seen that the development of the body of the imago proceeds from distinct formative centres (imaginal discs) already present in the larva, having appeared during embryonic life. We have met with such imaginal discs in connection with the different parts of the head, the limbs, the hypodermis, and the various parts of the intestinal canal. We have seen that the development of the mesodermal organs of the imago (muscles, connective tissue, fat-body) proceeds from a mesodermal part of the imaginal discs, the first origin of which, however, is still somewhat obscure. Simultaneously with the building up of the imaginal organs, we have the destruction of the larval organs through the action of the phagocytes. These two processes (disintegration and regeneration) go on side by side in such a way that the continuity of the organ is in most cases perfectly preserved, complete disintegration of the larval tissue only occurring after the development of the permanent organ. The musculature of the larva here forms an exception, as it undergoes disintegration very early.

We must, in conclusion, once more point out that the sharp distinction between the larval, the pupal, and the imaginal stages seems to be founded only upon the appearance of the external surface of the body, as resulting from the consecutive moults. The phenomena of internal development, on the contrary, represent a complete, continuous series of transformations, which do not show any such abrupt changes. We can, however, in the main, distinguish, according to the vital functions belonging to them, the forms of the larval, the pupal, and the imaginal stages.

III. Parthenogenesis, Paedogenesis, Heterogeny.

A capacity for developing unfertilised eggs in a parthenogenetic manner has repeatedly been observed in the Insecta. Parthenogenesis may here be either occasional (*e.g.*, many Lepidoptera, *Bombyx*, *Liparis*) or may be of normal occurrence, often recurring at fixed intervals in the ontogenetic cycle.* The males of the social Wasps and Bees, for instance, are produced from eggs that develop parthenogenetically. This is also the case in the Ants, and in *Nematus* and other *Tenthredinidae*, while, in the *Cynipidae*, only females are produced from the parthenogenetic eggs. In the Lepidoptera it seems to be the rule that females come from the parthenogenetic eggs. In *Psyche* and *Solenobia*, for example, a succession of many parthenogenetic generations was observed, while males were only seldom met with. The same is the case in *Apatania* among the Trichoptera (KLAPALEK). In certain *Cynipidae* there is a cyclic alternation of parthenogenetic females and male and female sexual forms of a different shape (true heterogeny). There thus develops, in the galls produced by a form known as *Spathegaster baccarum*, a gall-wasp of different shape called *Neuroterus ventricularis*, of which only parthenogenetic females are known. The unfertilised eggs laid by *Neuroterus*, which develop in peculiarly shaped galls, give rise again to the sexual generation of *Spathegaster*.

With the possibility of attaining reproduction by means of unfertilised eggs is connected the shifting back of this process to an early stage of development (*paedogenesis*). Thus, according to GRIMM, in one species of *Chironomus*, the pupa lays eggs, while other Diptera (*Cecidomyia*), even as larvae, are capable of reproducing themselves parthenogenetically and viviparously. The parthenogenetic reproduction of the *Aphidae* must also to some extent be regarded as paedogenesis; in these Insects it may happen that the embryo produced parthenogenetically may in its turn reproduce itself.

The *heterogeny* of the Phytophthires seems to be founded on the

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* [In this connection NUSSBAUM (No. XXXV.) has recently made a series of careful experiments on certain Lepidoptera, viz., *Bombyx*, *Porthesia*, and *Liparis*. He only succeeded in demonstrating the parthenogenetic condition in *Bombyx*, in which form two per cent. of the unfertilised eggs (1100) showed segmentation, but never hatched.—ED.]

definite alternation of a generation of parthenogenetic females with a normal generation of males and females, the latter generation reproducing the former by means of a fertilised egg, these generations being distinguished from each other by certain features in the structure of the body. In the *Aphidae*, the hibernating fertilised winter-eggs yield in spring a generation that reproduces itself parthenogenetically and viviparously, and which is followed during the spring and summer by a series of generations reproducing themselves in the same way, the individuals of which are often winged, but may also be wingless. This series is closed towards autumn by a generation known as the *sexupara*, the parthenogenetic and viviparous descendants of which are, as a rule, winged males and wingless females. After copulation has taken place, the female lays the fertilised winter-eggs, from which, in the next spring, the first generation capable of parthenogenetic reproduction hatches. Under certain circumstances it, however, appears that single individuals of the parthenogenetic generations are able to hibernate, and to give origin in the spring to a new parthenogenetic series. In the same way, among other Phytophthires, there are often parallel series of cycles of generations (DREYFUSS, No. 137).

A further complication in the cycle of development of the *Aphidae* is brought about in connection with frequent migration from one plant to another. A winged parthenogenetic generation frequently appears, and then may migrate to a different plant, there to reproduce itself, and in a later generation returns to the original host. These wandering generations, the occurrence of which was often pointed out by LICHTENSTEIN, have been distinguished as *emigrantes*, *alienicolae*, and *remigrantes* by BLOCHMANN (No. 135). In *Pemphigus terebinthi*, for example, according to DERBÈS, the fertilised egg gives rise to a wingless parthenogenetic generation (I.), which produces another winged generation (II., emigrantes). This generation leaves the place occupied up to this time and produces a third generation (III., remigrantes = sexupara), which, after hibernating, returns to the original host and produces the small, mouthless, wingless sexual animals without intestine (IV., sexuales). The cycle of generations in *Pemphigus terebinthi* is interesting because the sexual generation does not here occur, as it usually does, in the autumn, but in the spring, being produced by hibernating parthenogenetic forms.

Conditions similar to those in the *Aphidae* are found in the *Chermetidae*, which have recently been much investigated. The chief distinction between the two is that here the parthenogenetic, like the sexual generation, is also oviparous. In *Phylloxera quercus*, according to LICHTENSTEIN, the winter-eggs that are laid on *Quercus coccifera* give rise to a mother animal (*fundatrix*), which produces parthenogenetically a winged generation capable of parthenogenetic reproduction (emigrantes); these wander over to the leaves of *Quercus pedunculata* and *Q. pubescens*. Several wingless generations (alienicolae) now follow, which reproduce parthenogenetically, the return to *Quercus coccifera* being finally made possible by the production of the winged sexupara. The eggs laid by the sexupara here give rise to the wingless sexual generation devoid of proboscis and intestinal canal, which lays the winter-eggs. In *Phylloxera vastatrix*, the young animals that develop out of the winter-eggs laid beneath the bark of the trunk wander to the root, there to give origin parthenogenetically to several generations of wingless *Phylloxera*, which cause the swellings on the root. The series of these generations closes by the production of winged sexupara, which wander up the trunk and swarm. These forms also are parthenogenetic. Their eggs, which vary in size according to the sex of the developing embryo, yield sexual animals devoid of proboscis, intestine, and wings, which produce the winter-eggs. Parallel series are introduced into this cycle of generations also, *e.g.*, the wingless *Tetraneura*, living on leaves which run parallel with the generations of *Rhizobia*. In the cycle of generations of the genus *Chermes* recently investigated by BLOCHMANN (Nos. 134 and 135), DREYFUSS (No. 137), and CHOLODKOVSKY, similar conditions are found, but these are in some respects still very obscure. In *Chermes abietis*, the fertilised egg gives rise to a wingless parthenogenetic female (fundatrix, I.), which hibernates at the base of the buds of the fir-tree and, by piercing the buds, deforms them into galls. From this generation is produced a second (II.) consisting of winged parthenogenetic forms, some of which migrate to the larch and there give rise to a wingless generation (III.) which feeds on the needles and hibernates beneath the bark. These parthenogenetic alienicolae, in the following spring (the second year of the cycle), produce the winged remigrantes (IV.) or sexupara, which return to the fir-tree and there produce the wingless female and male, the fertilised eggs of which give rise once more to a fundatrix (I.). This cycle also is accompanied by a parallel series of forms that do not emigrate to the larch, but remain on the fir-tree.

IV. General Considerations.

It can hardly be doubted that the Insects and the Myriopoda are very intimately related. If it is considered that the anatomical features possessed in common and the similarity in development (although, indeed, the ontogeny of the Myriopoda is only partly known) are not sufficient to establish this relationship, great stress can be laid on the presence of transition-types, such as the Symphyla (*Scolopendrella*, Fig. 192) and Thysanura (*Campodea*, Fig. 193), which connect the two groups. It has only to be pointed out here that in the Thysanura, which are most intimately connected with the Orthoptera, we have, in the absence of wings and in the presence of the sac-like protrusible ventral sac, a recurrence of morphological characters which, while they are wanting in the higher Insects, are nevertheless found in the Myriopoda. On the other hand, the Myriopoda are closely related to *Peripatus*, so that we are justified in regarding the Onychophora, the Myriopoda, and the Insecta as belonging to a single phyletic ontogenetic series, which, through *Peripatus*, is linked on to the hypothetical racial form of the

Arthropoda (Protostraca) and, through the latter, to the Annelida (*cf.* Vol. ii., p. 315, and Vol. iii., p. 427).

The Insecta represent the highest grade of development of this phyletic series. That they are more highly specialised than the Myriopoda can be seen in the sharper demarcation of the different regions of the body, the fixation of the number of body-segments, and the development of a new locomotory system, the wings.

The marking-off of the three regions which can be distinguished in the body of the Insect (head, thorax, and abdomen) seems to be foreshadowed in the Myriopoda. Here also we find an anterior region, the head, sharply distinguished from the rest of the body. Further, of the trunk-segments that follow this region, the anterior (thoracic) segments may be distinctly differentiated from those which follow (the abdominal region); thus, by way of example, we may recall the fact that in the Diplopoda the thoracic segments do not unite to form double segments, as is the case with the other trunk-segments. We have, however, already pointed out (p. 236) that the region here distinguished as the thorax cannot be entirely identified with the thorax of the Insecta, since, in the Diplopoda, a limbless segment is intercalated between the three limb-bearing segments of the thorax (Fig. 121 *B*, p. 235, and Fig. 122, p. 237), a modification not found in the Insecta.

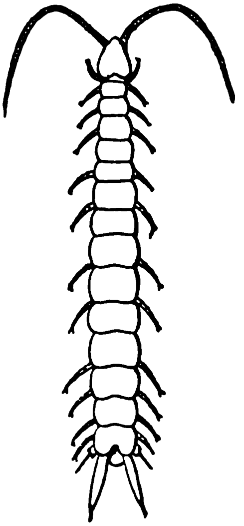

Fig. 192.—*Scolopendrella immaculata* (after Latzel, from Lang's *Text-book*).

Although the division of the body into regions can also be recognised as indicated in the Myriopoda, it is much more distinctly marked in the Insecta. The boundary between the thorax and the abdomen especially is much more distinct. This is connected with the division of labour between the two regions. In the Insecta, the most important locomotory organs are concentrated in the thoracic region. This has led to the greater rigidity of the thorax and the development of large masses of muscle, while the softer, more extensible abdominal region is the receptacle for almost all the vegetative organs. Into this region have shifted the most important parts of the intestinal canal and of the respiratory and circulatory systems, as well as the genital organs.

It should be mentioned that the boundary between the thoracic and abdominal regions is, in many Insect larvae, less sharply marked. This is connected with the fact that, in larvae, the thorax is frequently of less significance for the locomotion of the whole body than in the imagines, either because locomotory organs develop on the abdomen also (*e.g.*, in caterpillars), or that such organs are altogether wanting on the thorax as well (maggot-shaped larvae). More careful examination, especially of the inner organs, will, however, reveal in these cases also important differences between the thoracic and the abdominal segments. As we find that the separation of the thorax from the abdomen is very marked in the Thysanura, we may regard it as a feature inherited long ago by the Insect phylum, and may consider the apparent obliteration of these boundaries in certain larval forms as merely a secondary phenomenon.

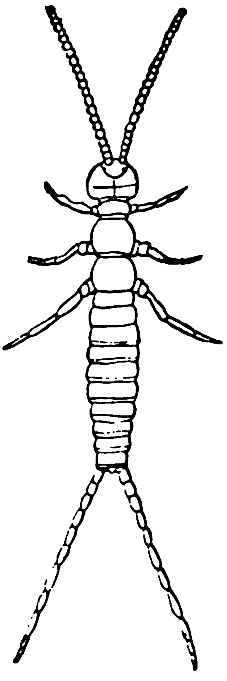
FIG. 198.—*Campodea staphylinus* (after LUBBOCK, from LANG'S *Text-book*).

The loss of extremities in the abdominal region is an important feature which distinguishes the Insecta from the Myriopoda. With regard to the derivation of the Insecta from the latter group, or from forms resembling the Myriopoda, the fact that the rudiments of abdominal extremities appear in the insect embryo and disappear later is of importance (pp. 296–300). The ventral stylets found on the abdomen in the Thysanura have repeatedly been regarded as vestiges of extremities, and this seems all the more probable as, in *Machilis*, these stylets actually function as locomotory organs. Recently, however, following HAASE (No. 153), and supported by the occurrence of similar stylets on the coxae of the thoracic limbs of *Machilis*, and on most of the limbs in *Scolopendrella*, zoologists have been inclined to regard these appendages merely as coxal spurs (p. 299). On the first abdominal segment of *Campodea*, on the contrary, there is a true limb-rudiment.

While, in the Myriopoda, the number of the body-segments varies greatly in the different genera and species, the number seems to be fixed and universally prevalent in the Insecta. The thorax is always composed of three segments, each of which carries a pair of legs (a fact which gave rise to the name of Hexapoda). In the same way it seems to be clearly established by ontogeny that the abdominal region is universally composed of ten trunk-segments and one subsequent anal segment (telson). Greater difficulty arises in reckoning the number of segments which have been drawn into the formation of the head. Three maxillary segments (a mandibular and a first and second maxillary segment) here combine with an anterior primary cephalic section. The segmentation of the brain leads us to suppose that the latter is composed of three segments (p. 325), while between this section and the mandibular segment a vestigial so-called pre-maxillary segment seems to be intercalated. In reckoning the segments here, however, we are on somewhat hypothetical ground. It may be mentioned that the antennae belong to the second brain-segment, and, by their originally post-oral position, as well as by their relation to the coelomic sacs belonging to that segment (in Orthoptera, p. 295), in all respects resemble true trunk-limbs. This is in entire agreement with what has been learnt of these limbs in connection with *Peripatus* and the Myriopoda.

One of the most interesting questions in the phylogeny of the Insecta is that of the rise of the wings. The rudiments of the wings appear on the meso- and meta-thorax as dorsal integumental outgrowths, the inner cavities of which receive later the tracheal ramifications. It is an interesting fact that similar lateral fold-like widenings of the dorsal plates, which recall the first rudiments of wings, also occur on the pro-thorax (*Machilis* and *Blatta*). These are most clearly visible on the larvae of *Calotermes* (Fig. 194, F. MÜLLER, No. 158), in the youngest stages of which outgrowths of the pro-thorax and meso-thorax are first evident, these being originally devoid of tracheae. While the anterior pair of these outgrowths degenerates, the posterior pair is supplied with tracheae, and is thus transformed into the rudiment of the fore-wing, the rudiment of the hind-wing appearing simultaneously on the meta-thorax. The great similarity in position and structure between the wing-rudiments and the leaf-shaped tracheal gills, as found on the abdominal segments of the Ephemerid larvae (Fig. 177, *k*, p. 358), has led to many attempts to consider them as homodynamous structures. This view, which was adopted by GEGENBAUER and LUBBOCK (No. 156), has recently also received the support of REDTENBACHER (No. 165). F. MÜLLER, who also supports the above, is inclined to hold that the original function of the wings was respiratory. This view, which seems well supported by the structure of the wing-rudiments, within which are found blood-spaces and tracheal ramifications, involves the assumption that the winged Insects are derived from an aquatic form. The phyletic series mentioned above, leading from *Peripatus* through the Myriopoda and Thysanura to the Orthoptera, contains throughout only forms living on land and adapted for terrestrial life. We have no reason for assuming that an aquatic ancestral form has been introduced into the series of ancestors of the winged Insecta (Pterygogenea). The manner of life of the aquatic larval forms of the Hemimetabola, as well as their respiratory organs, which are suited to life in water, must be regarded as secondarily acquired. For the same reasons we cannot adopt the view of DOHRN, who, going still further back in the phyletic series, is inclined to refer the tracheal gills of the Ephemerid larvae as well as the wing-rudiments to the elytra of the Annelidan ancestors of the Insecta (DOHRN, the Pantopoda). It must be pointed out that, in *Peripatus*, as well as in the Myriopoda, corresponding integumental folds are altogether wanting. We therefore consider that GRASSI (No. 150) is justified in regarding these organs as new acquisitions by the Insectan phylum, and in tracing them back to integumental outgrowths of the lateral margins of the tergal plates that have been constricted off and have become independent, the wing-musculature being derived from the system of dorso-ventral muscles, which is also represented in the other segments of the body. We may perhaps assume that the transition from the creeping method of locomotion to flight was made through the acquisition of a climbing habit, in which distances would occasionally be overcome by springing, a circumstance which gave rise to the development of parachute-like widenings of the thoracic segments. The transition from such integumental folds, used as a parachute but still immovable, to independent active locomotory organs seems to us fairly plausible. It is perhaps not without significance that the capacity for rising above the surface on which they rest is common among the Thysanura, the Collembola, and the Orthoptera, and that in the latter (*e.g.*, in *Psophus stridulus*) the wings are scarcely used otherwise than as parachutes. The limitation of wings to the meso- and

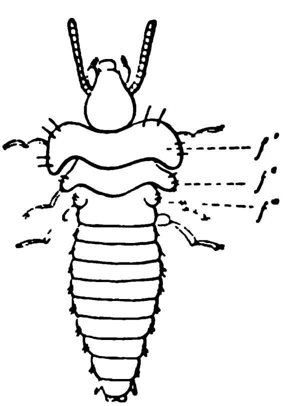

FIG. 194. -- Larvae of *Calotermes rugosus* (after F. MÜLLER). *f'*, wing-like appendages of the prothorax; *f''*, rudiment of the fore-wing; *f'''*, rudiment of the hind-wing.

meta-thorax may be connected with the position of the centre of equilibrium of the body. We agree with **Brauer** (No. 146) in considering the wingless condition as a primary characteristic only in the Apterygogenea, whereas in those wingless orders of Insects (the Mallophaga, Siphonaptera, etc.) which are placed with the Pterygogenea it must be regarded as secondarily acquired.

The segmental arrangement of the tracheal stigmata should be noted. It appears that originally a pair of stigmata occurred on each of the three thoracic segments, as well as the eight following abdominal segments, at least, the respiratory system of the Thysanura, as investigated by **Grassi** and **Haase**, is favourable to such an assumption. In most Insecta, however, the number of thoracic stigmata is reduced. There does not appear to be a true pair of stigmata in the head. We have already given the reasons (pp. 323 and 335) why neither the endoskeletal invaginations of the head nor the salivary glands can be regarded as homodynamous with the tracheal invaginations. It should, however, be mentioned, on the other hand, that the presence of a pair of stigmata belonging to the head has been maintained in *Scolopendrella* (**Haase**) and in *Sminthurus* (**Lubbock**).

We have still to mention the *compound eyes* (*facet-eyes*) as one of the features which raise the Insecta to a higher level than the Myriopoda. The most primitive form of eye in the Insecta is evidently represented by the ocellus (Fig. 165, p. 332), the structure of which, according to **Grenacher** (No. 151), may still, in a few cases, be traced back direct to the simple cup-shaped eye, while, in other cases, through the development of a vitreous body-layer (lentigen layer), it becomes a bilaminar complicated eye (Fig. 164 *B*, p. 331). We shall hardly err in deriving the Insectan ocellus direct from the cup-shaped eyes of the Annelida (**Kennel**, No. 154). The compound eye, on the contrary, appears to correspond to an accumulation of ocelli, in which the number of ocelli has been increased while the single ommatidia have sunk to a lower level of functional capacity. We have already seen (p. 242) that, in the Myriopoda, an almost complete series of transitions is to be found between the aggregations of ocelli and the true facet-eyes. We shall therefore be justified in assuming this derivation as highly probable for the facet-eyes of the Insecta. For the relation of the facet-eye to the ocelli of the same animal, *cf.* p. 333. Bearing in mind the fact that *Machilis* already possesses facet-eyes, we must regard the latter as a somewhat ancient acquisition among the ancestors of the Insecta, and shall feel inclined to regard the absence of the facet-eye (whether in larvae or in imagines) as the result of degeneration.

We must, in conclusion, point out a few more important factors in the embryonic development of the Insecta. The first of these is the development of the embryonic envelopes, the acquisition of which (like the development of flying) proves the Insecta to be the most highly developed of all Arthropods. It therefore seems remarkable that the Insecta in other respects, especially with regard to the way in which the germ-layers form, have retained very primitive characters. The long blastopore which extends over the whole of the ventral side, the presence of a distinct invagination-gastrula which leads to the development of an archenteric tube, and the manner in which the mesoderm separates from the entoderm must here be mentioned in this connection. With regard to the last point, it should be mentioned that the separation of the mesoderm from the entoderm is accomplished by a process which can be traced back to that of infolding, so that Kowalevsky (No. 49) quite correctly compared the formation of the germ-layers in the Insecta with their formation in *Sagitta*, a proceeding in which he was afterwards supported by Rabl. The coelomic sacs of the Insecta may thus, according to their development, be regarded as archenteric diverticula. Another point of interest is the transformation undergone in later stages by the primitive segments, which were treated in detail in the chapter on the development of the heart and the genital organs.

LITERATURE.

Embryonic Development.

Older treatises by Herold, Kollicker, Leuckart, Rathke, Robin, Suckow, and Zaddach.

1. Ayers, H. On the development of Oecanthus niveus and its parasite Teleas. *Mem. Boston Soc. Nat. Hist.* Vol. iii. 1884.
2. Balbiani, E. G. Sur la signification des cellules polaires des Insectes. *Compt. Rend. Acad. Sci. Paris.* Tom. xcv. 1882.
3. Balbiani, E. G. Contribution à l'étude de la formation des organes sexuels chez les Insectes. *Recueil Zool. Suisse.* Tom. ii. 1885.
4. Barrois, J. Développement des Podurelles. *Assoc. Franç. Avanc. Sci.* 7e Sess. 1879.

5. Blochmann, F. Ueber die Richtungskörper bei Insecteneiern. *Morph. Jahrb.* Bd. xii. 1887.

6. Bobretzky, N. Ueber die Bildung des Blastoderms und der Keimblätter bei Insecten. *Zeitschr. f. Wiss. Zool.* Bd. xxxi. 1878.

7. Brandt, A. Beiträge zur Entwicklungsgeschichte der Libelluliden und Hemipteren. *Mém. Acad. St. Pétersbourg* (7). Tom. xiii. 1869.

8. Brandt, A. Ueber das Ei und seine Bildungsstätte. *Leipzig*, 1878.

9. Brandt, A. Commentare zur Keimbläschentheorie des Eies. I. Die Blastoderm-elemente und Dotterballen der Insecten. *Archiv. f. Mikro. Anat.* Bd. xvii. 1880.

10. Bruce, A. T. Observations on the Embryology of Insects and Arachnids. A memorial volume. *Baltimore*, 1887.

11. Bütschli, O. Zur Entwicklungsgeschichte der Biene. *Zeitschr. f. Wiss. Zool.* Bd. xx. 1870.

12. Bütschli, O. Bemerkungen über die Entwicklungsgeschichte von Musca. *Morph. Jahrb.* Bd. xiv. 1888.

13. Carrière, J. Die Entwicklung der Mauerbiene (Chalicodoma muraria Fabr.) im Ei. *Archiv. f. Mikro. Anat.* Bd. xxxv. 1890.

14. Carrière, J. Kurze Mittheilungen aus fortgesetzten Untersuchungen über die Sehorgane. 7. Die Entwicklung und die verschiedenen Arten der Ocellen. *Zool. Anz.* Jahrg. ix. 1886.

15. Carrière, J. Die Drüsen am ersten Hinterleibsringe der Insectenembryonen. *Biol. Centralbl.* Bd. xi. 1891.

16. Cholodkovsky, N. A. Ueber die Bildung des Entoderms bei Blatta germanica. *Zool. Anz.* Jahrg. xi. 1888.

17. Cholodkovsky, N. A. Zur Embryologie von Blatta germanica. *Zool. Anz.* Jahrg. xiii. 1890.

18. Cholodkovsky, N. A. Zur Embryologie der Hausschabe (Blatta germanica). *Biol. Centralbl.* Bd. x. 1890.

19. Cholodkovsky, N. A. Studien zur Entwicklungsgeschichte der Insecten. *Zeitschr. f. Wiss. Zool.* Bd. xlviii. 1889.

20. Cholodkovsky, N. A. Ueber die Entwicklung des centralen Nervensystems bei Blatta germanica. *Zool. Anz.* Jahrg. xiv. 1891.

20a. Cholodkovsky, N. A. Die Embryonalentwicklung von Phyllodromia (Blatta) germanica. *Mém. Acad. St. Pétersbourg* (7). Tom. xxxviii. 1891. (Seen only after this volume had been printed.)

21. Dohrn, A. Notizen zur Kenntniss der Insectenentwicklung. *Zeitschr. f. Wiss. Zool.* Bd. xxvi. 1876.
22. Ganin, M. Beiträge zur Erkenntniss der Entwicklungsgeschichte bei den Insecten. *Zeitschr. f. Wiss. Zool.* Bd. xix. 1869.
23. Ganin, M. Ueber die Embryonalhülle der Hymenopteren- und Lepidopterenembryonen. *Mém. Acad. St. Pétersbourg* (7). Tom. xiv. 1870.
24. Graber, V. Vorläufige Ergebnisse einer grösseren Arbeit über vergl. Embryologie der Insecten. *Archiv. f. Mikro. Anat.* Bd. xv. 1878.
25. Graber, V. Ueber die Polypodie bei Insectenembryonen. *Morph. Jahrb.* Bd. xiii. 1888.
26. Graber, V. Ueber die primäre Segmentirung des Keimstreifs der Insecten. *Morph. Jahrb.* Bd. xiv. 1888.
27. Graber, V. Vergleichende Studien über die Keimhüllen und die Rückenbildung der Insecten. *Denkschr. Acad. Wiss. Wien.* Bd. lv. 1888.
28. Graber, V. Vergleichende Studien über die Embryologie der Insecten und insbes. der Musciden. *Denkschr. Acad. Wiss. Wien.* Bd. lvi. 1889.
29. Graber, V. Ueber den Bau und die phylogenetische Bedeutung der embryonalen Bauchanhänge der Insekten. *Biol. Centralbl.* Bd. ix. 1889.
30. Graber, V. Vergleichende Studien am Keimstreif der Insecten. *Denkschr. Acad. Wiss. Wien.* Bd. lvii. 1890.
31. Graber, V. Ueber die embryonale Anlage des Blut- und Fettgewebes der Insecten. *Biol. Centralbl.* Bd. xi. 1891.
32. Grassi, B. Intorno allo sviluppo delle api nell' uovo. *Atti Acad. Gioenia Sci. Nat. Catania* (3). Tom. xviii. 1884.
33. Grassi, B. Breve nota intorno allo sviluppo degli Japyx. *Catania*, 1884. See also: I. Progenitori degli Insetti e dei Miriopodi. 1. L'Japyx e la Campodea. *Atti Acad. Gioenia Sci. Nat. Catania* (3). Tom. xix. 1885.
34. Hallez, P. Orientation de l'embryon et formation du cocon chez la Periplaneta orientalis. *Compt. Rend. Acad. Sci. Paris.* Tom. ci. 1885.
35. Hallez, P. Sur la loi de l'orientation de l'embryon chez les Insectes. *Compt. Rend. Acad. Sci. Paris.* Tom. ciii. 1886.
36. Hatschek, B. Beiträge zur Entwicklungsgeschichte der Lepidopteren. *Jen. Zeitschr. f. Naturw.* Bd. xi. 1877.

37. **Heider**, K. Ueber die Anlage der Keimblätter von Hydrophilus piceus L. *Abh. k. Acad. Wiss. Berlin*, 1885.

38. **Heider**, K. Die Embryonalentwicklung von Hydrophilus piceus L. Theil. i. *Jena*, 1889.

39. **Henking**, H. Die ersten Entwicklungsvorgänge im Fliegenei und freie Kernbildung. *Zeitschr. f. Wiss. Zool.* Bd. xlvi. 1888.

40. **Henking**, H. Ueber die Bildung von Richtungskörpern in den Eiern der Insecten und deren Schicksal. *Nachr. Ges. Wiss. Göttingen*, 1888.

41. **Hertwig**, O. and R. Die Coelomtheorie. Versuch einer Erklärung des mittleren Keimblattes. *Jena*, 1881.

42. **Heymons**, R. Ueber die hermaphroditische Anlage der Sexualdrüsen beim Männchen von Phyllodromia (Blatta) germanica. *Zool. Anz.* Jahrg. xiii. 1890.

43. **Heymons**, R. Die Entstehung der Geschlechtsdrüsen von Phyllodromia (Blatta) germanica L. In.-Diss. *Berlin*, 1891.

44. **Jordan**, K. Anatomie und Biologie der Physapoda. *Zeitschr. f. Wiss. Zool.* Bd. xlvii. 1888.

45. **Kadyi**, H. Beitrag zur Kenntnis der Vorgänge beim Eierlegen der Blatta orientalis. *Zool. Anz.* Jahrg. ii. 1879.

46. **Korotneff**, A. Entwicklung des Herzens bei Gryllotalpa. *Zool. Anz.* Jahrg. vi. 1883.

47. **Korotneff**, A. Die Embryologie der Gryllotalpa. *Zeitschr. f. Wiss. Zool.* Bd. xli. 1885.

48. **Kowalevsky**, A. Embryologische Studien an Würmern und Arthropoden. *Mém. Acad. St. Pétersbourg* (7). Bd. xvi. 1871.

49. **Kowalevsky**, A. Zur embryonalen Entwicklung der Musciden. *Biol. Centralbl.* Bd. vi. 1886.

50. **Kupffer**, C. Ueber das Faltenblatt an den Embryonen der Gattung Chironomus. *Archiv. f. Mikro. Anat.* Bd. ii. 1866.

51. **Lemoine**, V. Recherches sur le développement des Podurelles. *Ass. Franç. Avanc. Sci. Congrès de la Rochelle.* 1882.

52. **Leuckart**, R. Ueber die Micropyle und den feineren Bau der Schalenhaut bei den Insecteneiern. *Archiv. f. Anat. u. Phys.* 1855.

53. **Melnikoff**, N. Beiträge zur Embryonalentwicklung der Insecten. *Archiv. f. Naturg.* Bd. xxxv. 1869.

54. **Metschnikoff**, E. Untersuchungen über die Embryologie der Hemipteren. *Zeitschr. f. Wiss. Zool.* Bd. xvi. 1866.

55. **Metschnikoff**, E. Embryologische Studien an Insecten. *Zeitschr. f. Wiss. Zool.* Bd. xvi. 1866.

56. **Miall**, L. C., and **Denny**, A. The structure and life-history of the Cockroach (Periplaneta orientalis). *London*, 1886. (The section on embryonic development by **Nusbaum**.)

57. **Nusbaum**, J. Vorl. Mittheilung über die Chorda der Arthropoden. *Zool. Anz.* Jahrg. vi. 1883.

58. **Nusbaum**, J. Die Entwicklung der Keimblätter bei Meloë proscarabaeus. *Biol. Centralbl.* Bd. viii. 1888.

59. **Nusbaum**, J. Zur Frage der Segmentirung des Keimstreifs und der Bauchanhänge der Insectenembryonen. *Biol. Centralbl.* Bd. ix. 1889.

60. **Nusbaum**, J. Zur Frage der Rückenbildung bei den Insectenembryonen. *Biol. Centralbl.* Bd. x. 1890.

61. **Nusbaum**, J. On the development of the efferent ducts of the genital glands in the Insecta (Polish, with résumé in German, pp. 39–42). *Kosmos, Lemberg.* Jahrg. ix. 1884.

62. **Nusbaum**, J. Zur Entwicklungsgeschichte der Ausführungsgänge der Sexualdrüsen bei den Insecten. *Zool. Anz.* Jahrg. v. 1882.

63. **Nusbaum**, J. The Embryology of Meloë proscarabaeus, Marscham (Polish, with Latin explanation of plates). *Kosmos, Lemberg.* 1891.

64. **Packard**, A. S. Embryological Studies on Diplax, Perithemis, and the thysanurous genus Isotoma. *Mem. Peabody Acad. Sci.* Vol. i. 1871.

65. **Patten**, W. The development of Phryganids, with a preliminary note on the development of Blatta germanica. *Quart. Journ. Micro. Sci.* Vol. xxiv. 1884.

66. **Patten**, W. Studies on the eyes of Arthropods. Development of the eyes of Vespa, with observations on the Ocelli of some Insects. *Journ. Morphol. Boston.* Vol. i.

67. **Patten**, W. Studies on the eyes of Arthropods. II. Eyes of Acilius. *Journ. Morphol. Boston.* Vol. ii. 1888.

68. **Patten**, W. On the origin of Vertebrates from Arachnids. *Quart. Journ. Micro. Sci.* (2). Vol. xxxi. 1890.

69. **Pedaschenko**, D. On the formation of *Notonecta glauca* (Russian). *Revue Sci. Nat. St. Pétersbourg.* Année i. 1891.

70. **Platner**, G. Die erste Entwicklung befruchteter und parthenogenetischer Eier von Liparis dispar. *Biol. Centralbl.* Bd. viii. 1888.

71. Ritter, R. Die Entwicklung der Geschlechtsorgane und des Darmes bei Chironomus. *Zeitschr. f. Wiss. Zool.* Bd. l. 1890.

72. Ryder, J. A. The development of Anurida maritima Guerin. *Amer. Natur.* Vol. xx. 1886.

73. Schmidt, F. Die Bildung des Blastoderms und des Keimstreifs der Musciden. *Sitz. Naturf. Ges. Dorpat.* Bd. viii. 1889.

74. Schneider, A. Ueber die Entwicklung der Geschlechtsorgane der Insecten. *Zool. Beiträge, v. A. Schneider.* Bd. i. 1883.

75. Selvatico, D. S. Sullo sviluppo embrionale dei Bombicini. *Boll. Bachicoltura.* Ann. viii. 1881.

76. Sommer, A. Ueber Macrotoma plumbea. *Beiträge zur Anatomie der Poduriden. Zeitschr. f. Wiss. Zool.* Bd. xli. 1885.

77. Stuhlmann, F. Die Reifung des Arthropodeneies nach Beobachtungen an Insecten, Spinnen, Myriopoden und Peripatus. *Ber. Freib. Naturf.-Gesellsch.* Bd. i. 1886.

78. Tichomiroff, A. Ueber die Entwicklungsgeschichte des Seidenwurms. *Zool. Anz.* Jahrg. ii. 1879.

79. Tichomiroff, A. On the Ontogeny of the Bombyx mori within the egg (Russian). *Izvyest. imp. Obshch. Lyubit. Estest. Antrop. i. Ethnog. Moscow.* Tom. xxxii., 4. 1882.

80. Tichomiroff, A. Ueber die Entwicklung der Calandra granaria. *Biol. Centralbl.* Bd. x. 1890.

81. Tichomirowa, O. S. Zur Embryologie von Chrysopa. *Biol. Centralbl.* Bd. x. 1890.

82. Uljanin, V. Notes on the Ontogeny of the Poduridae (Russian). *Isvyest. imp. Obshch. Lyubit. Estestv. Antrop. i. Ethnog. Moscow.* Tom. xvi. 1875.

83. Uljanin, V. Sur le développement des Podurelles. *Archiv. Zool. Expér.* Tom. iv. 1875. Tom. v. 1876.

84. Viallanes, H. Sur quelques points de l'histoire du développement embryonnaire de la Mante religieuse. *Prelim. Conr. Rev. Biol. du Nord de la France.* Tom. ii. 1889–1890.

85. Voeltzkow, A. Entwicklung im Ei von Musca vomitoria. *Arb. Zool. Zoot. Inst. Würzburg.* Bd. ix. 1889.

86. Voeltzkow, A. Melolontha vulgaris, ein Beitrag zur Entwicklung im Ei bei Insecten. *Arb. Zool. Zoot. Inst. Würzburg.* Bd. ix. 1889.

87. Weismann, A. Die Entwicklung der Dipteren im Ei, nach Beobachtungen an Chironomus sp., Musca vomitoria und Pulex canis. *Zeitschr. f. Wiss. Zool.* Bd. xiii. 1865.

88. Weismann, A. Zur Embryologie der Insecten. *Archiv. f. Anat. u. Physiol.* 1864.

89. Weismann, A. Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insectenei. *Beiträge z. Anat. u. Embryol. etc. Bonn*, 1882.

90. Weismann, A., and Ischikawa, Ch. Ueber die Bildung der Richtungskörper bei thierischen Eiern. *Ber. Naturf. Ges. Freiburg.* Bd. iii. 1887.

91. Wheeler, W. M. On the Appendages of the first Abdominal Segment of the Embryo Cockroach (Blatta germanica). *Proc. Wiscons. Acad. Sci.* Vol. viii. 1890.

92. Wheeler, W. M. Ueber drüsenartige Gebilde im ersten Abdominalsegment der Hemipterenembryonen. *Zool. Anz.* Jahrg. xii. 1889.

93. Wheeler, W. M. Ueber ein eigenthümliches Organ im Locustidenembryo (Xiphidium ensiferum). *Zool. Anz.* Jahrg. xiii. 1890.

94. Wheeler, W. M. Neuroblasts in the Arthropod Embryo. *Journ. Morphol. Boston.* Vol. iv. 1891.

95. Wheeler, W. M. The Embryology of Blatta germanica and Doryphora decemlineata. *Journ. Morphol. Boston.* Vol. iii. 1889.

96. Will, L. Zur Bildung des Eies und des Blastoderms bei den viviparen Aphiden. *Arb. Zool. Zoot. Inst. Würzburg.* Bd. vi. 1883.

97. Will, L. Entwicklungsgeschichte der viviparen Aphiden. *Zool. Jahrb. Abth. f. Anat.* Bd. iii. 1888.

98. Witlaczil, Em. Entwicklungsgeschichte der Aphiden. *Zeitschr. f. Wiss. Zool.* Bd. xl. 1884.

Postembryonic Development.

On pupal development *cf.* the older treatises of Swammerdam, Herold, and L. Agassiz.

99. Bemmelen, J. F. van. Ueber die Entwicklung von Farben und Adern auf den Schmetterlingsflügeln. *Tijdschrift der Nederlandsche Dierkundige Vereeniging* (2). Deel ii., Afl. iv. 1889.

100. Brauer, Fr. Die Zweiflügler des Kais. Museums zu Wien. III. Systemat. Studien auf Grundlage der Dipteren-Larven *Denkschr. Acad. Wiss. Wien.* Bd. xlvii.

101. **Brauer, Fr.**, and **Redtenbacher, Jos.** Ein Beitrag zur Entwicklung des Flügelgeäders der Insecten. *Zool. Anz.* Jahrg. xi. 1888.

102. **Dewitz, H.** Beiträge zur Kenntniss der postembryonalen Gliedmaassenbildung bei den Insecten. *Zeitschr. f. Wiss. Zool.* Bd. xxx. Suppl. 1878.

103. **Dewitz, H.** Ueber Bau und Entwicklung des Stachels und der Legescheide einiger Hymenopteren und der grünen Heuschrecke. *Zeitschr. f. Wiss. Zool.* Bd. xxv. 1875. Bd. xxviii. 1877.

104. **Dewitz, H.** Ueber die Flügelbildung bei Phryganiden und Lepidopteren. *Berl. Ent. Zeitschr.* Bd. xxv. 1881.

105. **Fabre, L.** L'hypermétamorphose et les mœurs des Méloides. *Ann. Sci. Nat.* (4). Vol. vii. 1857.

106. **Frenzel, J.** Einiges über den Mitteldarm der Insecten, sowie über Epithelregeneration. *Archiv. f. Mikro. Anat.* Bd. xxvi. 1885.

107. **Ganin, M.** On the post-embryonic development of the Insecta (Russian). *Warsaw*, 1876. *Syezd. Russk. Estestv. Vrachei v. Varshavye.* Abstract by **Hoyer.** *Jahresb. der Anat. und Phys. von Hoffmann und Schwalbe.* Bd. v. 1876. See also *Zeitschr. f. Wiss. Zool.* Bd. xxviii. 1877.

108. **Haase, E.** Zur Entwicklung der Flügelrippen der Schmetterlinge. *Zool. Anz.* Jahrg. xiv. 1891.

109. **Hurst, H.** The post-embryonic development of a gnat (Culex). *Trans. Liverpool Biol. Soc.* Vol. iv. 1890.

110. **Jacobi, A.** On the development of markings on the wings of the Lepidoptera (Russian). *Protok. Zasyed. Obshch. Estestv. pri imp. Kazanck. Univers.* 1888–89.

111. **Kowalevsky, A.** Beiträge zur nachembryonalen Entwicklung der Musciden. *Zool. Anz.* Bd. viii. 1885.

112. **Kowalevsky, A.** Beiträge zur Kenntniss der nachembryonalen Entwicklung der Musciden. Theil. i. *Zeitschr. f. Wiss. Zool.* Bd. xlv. 1887.

113. **Künckel d'Herculais, J.** Recherches sur l'organisation et le développement des Volucelles. *Paris*, 1875.

114. **Landois, H.** Beiträge zur Entwicklungsgeschichte der Schmetterlingsflügel in der Raupe und Puppe. *Zeitschr. f. Wiss. Zool.* Bd. xxi. 1871.

115. **Lowne, B. Th.** Anatomy, Physiology, Morphology, and Development of the Blow-Fly. *London.* Vol. i. 1890–92. Vol. ii. 1893–95.

116. **Metschnikoff, E.** Untersuchungen über intracelluläre Verdauung bei wirbellosen Thieren. *Arb. Zool. Inst. Wien.* Bd. v. 1883.

117. **Metschnikoff, E.** Untersuchungen über die mesodermalen Phagocyten einiger Wirbelthiere. *Biol. Centralbl.* Bd. iii. 1883.

118. **Müller, F.** Die Flügeladern der Schmetterlingspuppen. *Kosmos.* Jahrg. i. 1877.

119. **Pancritius, P.** Notiz über Flügelentwicklung bei den Insecten. *Zool. Anz.* Jahrg. vii. 1884.

120. **Pancritius, P.** Beiträge zur Kenntniss der Flügelentwicklung bei den Insecten. *Inaug.-Diss. Königsberg*, 1884.

121. **Rees, J. van.** Beiträge zur Kenntniss der inneren Metamorphose von Musca vomitoria. *Zool. Jahrb. Abth. f. Anat.* Bd. iii. 1888.

122. **Rees, J. van.** Over de post-embryonale ontwikkeling von Musca vomitoria. *Maandblad voor Natuurwetenschappen. Juli*, 1885.

123. **Rees, J. van.** Over intra-cellulaire spijsverteering en over de beteekenis der witte bloedlichampjes. *Maandblad voor Natuurwetenschappen.* Jaarg. xi. 1884.

124. **Rehberg, A.** Ueber die Entwickelung des Insectenflügels (in Blatta germanica). *Marienwerder.* 1886.

124a. **Schäffer, C.** Beiträge zur Histologie der Insecten. *Zool. Jahrb. Abth. f. Anat.* Bd. iii. 1889.

125. **Schiemenz, P.** Ueber das Herkommen des Futtersaftes und die Speicheldrüsen der Biene etc. *Zeitschr. f. Wiss. Zool.* Bd. xxxviii. 1883.

126. **Semper, C.** Ueber die Bildung der Flügel, Schuppen und Haare bei den Lepidopteren. *Zeitschr. f. Wiss. Zool.* Bd. viii. 1857.

127. **Verson, E.** Der Schmetterlingsflügel und die sog. Imaginalscheiben desselben. *Zool. Anz.* Jahrg. xiii. 1890.

128. **Viallanes, H.** Recherches sur l'histologie des Insectes et sur les phénomènes histologiques qui accompagnent le développement post-embryonnaire de ces animaux. *Ann. Sci. Nat.* (6). Tom. xiv. 1882.

129. **Weismann, A.** Die nachembryonale Entwicklung der Musciden nach Beobachtungen an Musca vomitoria und Sarcophaga carnaria. *Zeitschr. f. Wiss. Zool.* Bd. xiv. 1864.

130. **Weismann, A.** Die Metamorphose von Corethra plumicornis. *Zeitschr. f. Wiss. Zool.* Bd. xvi. 1866.

131. **Wielowiejsky**, H. v. Ueber den Fettkörper von Corethra plumicornis und seine Entwicklung. *Zool. Anz.* Jahrg. vi. 1881.

Parthenogenesis and Heterogeny.

132. **Adler**, H. Ueber den Generationswechsel der Eichen-Gallwespen. *Zeitschr. f. Wiss. Zool.* Bd. xxxv. 1881.

133. **Balbiani**, E. G. Observations sur la réproduction du Phylloxera du Chêne. *Ann. Sci. Nat.* (5). Vol. xix. 1874.

134. **Blochmann**, F. Ueber die Geschlechtsgeneration von Chermes abietis L. *Biol. Centralbl.* Bd. vii. 1887–88.

135. **Blochmann**, F. Ueber die regelmässigen Wanderungen der Blattläuse, speciell über den Generationscyclus von Chermes abietis L. *Biol. Centralbl.* Bd. ix. 1889.

136. **Carrière**, J. Die Reblaus. *Biol. Centralbl.* Bd. vii. 1888.

137. **Dreyfuss**, L. Ueber Phylloxerinen. *Wiesbaden*, 1889.

138. **Grimm**, O. v. Ungeschlechtliche Fortpflanzung einer Chironomus-Art und deren Entwicklung aus dem unbefruchteten Eie. *Mém. Acad. Pétersbourg.* 1870.

139. **Leuckart**, R. Die ungeschlechtliche Fortpflanzung der Cecidomyialarven. *Archiv. f. Naturg.* 1865.

140. **Leuckart**, R. Zur Kenntniss des Generationswechsels und der Parthenogenese bei den Insecten. *Frankfurt*, 1858.

141. **Lichtenstein**, J. Zur Biologie der Gattung Phylloxera. *Stettin. Entom. Zeitung.* Jahrg. xxxvi. 1875.

142. **Siebold**, C. Th. v. Beiträge zur Parthenogenesis der Arthropoden. *Leipzig*, 1871.

143. **Signoret**, V. Phylloxera de la Vigne. *Ann. Soc. Entomol. de France* (4). Tom. ix. 1869.

144. **Wagner**, N. Beitrag zur Lehre von der Fortpflanzung der Insectenlarven. *Zeitschr. f. Wiss. Zool.* Bd. xiii. 1863.

General.

145. **Brauer**, Fr. Verwandlung der Insecten im Sinne der Descendenz-Theorie. *Verh. Zool. Bot. Ges. Wien.* i. 1869. ii. 1870.

146. **Brauer**, Fr. Systematisch-zoologische Studien. *Sitzungsber. Akad. Wiss. Wien.* Bd. xci. 1885.

147. **Carrière**, J. Die Sehorgane der Thiere. *München und Leipzig*, 1885.

148. **Fernald**, H. T. The Relationships of Arthropods. *Johns Hopkins Univers. Stud. Biol. Lab.* Vol. iv. 1890.

149. **Graber, V.** Die Insecten. *München*, 1877. (*Die Naturkräfte*. Theil. ii. Vergl. Lebens- und Entwicklungsgeschichte der Insecten. 1879.)

150. **Grassi, B.** I progenitori dei Miriapodi e degli Insetti. Memoria viii. Anatomia comparata dei Tisanuri e considerazioni generali sull' organisazione degli Insetti. *Atti Acad. Lincei.* (4). Tom. iv. 1888. See also *Archiv. Ital. Biol.* Tom. xi. 1889.

151. **Grenacher, H.** Untersuchungen über das Sehorgan der Arthropoden, insbesondere der Spinnen, Insecten und Crustaceen. *Göttingen*, 1879.

152. **Haase, E.** Die Vorfahren der Insecten. *Abh. Ges. Isis. Dresden.* Bd. xi. 1887.

153. **Haase, E.** Die Abdominalanhänge der Insecten mit Berücksichtigung der Myriopoden. *Morph. Jahrb.* Bd. xv. 1890.

154. **Kennel, J. v.** Die Ableitung zunächst der sog. einfachen Augen der Arthropoden, nämlich der "Stemmata" der Insectenlarven, Spinnen, Scorpioniden etc. von Augen der Anneliden. *Sitzungsber. Nat. Ges. Dorpat.* Bd. viii. 1889.

155. **Korschelt, E.** Ueber die Entstehung und Bedeutung der versch. Zellenelemente des Insectenovariums. *Zeitschr. f. Wiss. Zool.* Bd. xliii. 1886.

156. **Lubbock, J.** Origin and Metamorphoses of Insects. *Nature Series. London*, 1883.

157. **Mayer, P.** Ontogenie und Phylogenie der Insecten. *Jen. Zeitschr. f. Naturwiss.* Bd. x. 1876.

158. **Müller, F.** Beiträge zur Kenntniss der Termiten. *Jen. Zeitschr. f. Naturwiss.* Bd. vii. 1873.

159. **Nassonow, N.** Welche Insectenorgane dürften homolog den Segmentorganen der Würmer zu halten sein? *Biol. Centralbl.* Bd. vi. 1886.

160. **Packard, A. S.** Guide to the Study of Insects, etc. *New York*, 1889.

161. **Palmén, J. A.** Zur Morphologie des Tracheensystems. *Helsingfors*, 1877.

162. **Palmén, J. A.** Zur vergleichenden Anatomie der Sexualorgane bei den Insecten. *Morph. Jahrb.* Bd. ix. 1883.

163. **Palmén, J. A.** Ueber paarige Ausführungsgänge der Geschlechtsorgane bei Insecten. Eine Monographische Untersuchung. *Helsingfors*, 1884.

164. **Ratzeburg, J. Th. C.** Die Forstinsecten. *Berlin*, 1837–1844.

165. **Redtenbacher**, Jos. Vergleichende Studien über das Flügelgeäder der Insecten. *Ann. Hofmus. Wien.* Bd. i. 1886.

166. **Westwood**, J. O. An introduction to the modern classification of Insects. *London*, 1839–1840.

APPENDIX TO LITERATURE ON INSECTA.

The Student will do well to consult **Packard's** *Text-book of Entomology* (1898), which deals most thoroughly with the morphology and ontogeny of the Insecta.

I. **Brüel**, L. Anatomie und Entwicklungsgeschichte der Geschlechtsausführwege sammt annexen von Calliphora erythrocephala. *Zool. Jahrb.* (*Anat.*). Bd. x. 1897.

II. **Carrière**, J. Die Entwicklungsgeschichte der Mauerbiene (Chalicodoma muraria) im Ei; herausg. u. vollendet von Otto Bürger. *Nova Acta Abh. d. k. Caes. Leop.-Akad.* Bd. xlix. 1897.

III. **Cholodkovsky**, N. A. Beiträge zu Monographie der Coniferen-Läuse. *Horae Soc. ent. Ross.* xxx.

IV. **Cholodkovsky**, N. A. Contributions à la theorie du mésoderme et de la métamérie. *Congr. Zool.* ii., 1. 1892.

V. **Cholodkovsky**, N. A. Embryonic development of Phyllodromia germanica (Russian). *Trud. St. Petersburg est.* xxii.

VI. **Cholodkovsky**, N. A. On the morphology and phylogeny of Insects. *Ann. Nat. Hist.* (6). Vol. x.

VII. **Cholodkovsky**, N. A. Zur Biologie der Lärchen-Chermes-Arten. *Zool. Anz.* Jahrg. xix., pp. 37–40.

Zur Kenntniss der auf Fichte (Picea excelsa) lebenden Lachnus-Arten. *T. c.* pp. 145–150.

VIII. **Claypole**, A. M. Some points on cleavage among Arthropods. *Trans. Amer. Micro. Soc.* Vol. xix. 1897.

IX. **Graber**, V. Beiträge zur vergleichenden Embryologie der Insecten. *Denkschr. Akad. Wien.* Bd. lviii.

IXa. **Graber**, V. Ueber die Morphologische Bedentung der ventralen abdominalanhänge der Insekten-Embryonen. *Morph. Jahrb.* Bd. xvii. 1892.

X. **Heider**, K. Ist der Keimblätterlehre erschüttert? *Zool. Centralbl.* Bd. iv. 1897.

XI. **Henking**, H. Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern der Insekten. Theil. i., ii., iii. *Zeitsch. f. Wiss. Zool.* Bd. xlix., li., liv.

XII. Henneguy, L. F. Contributions a l'embryogénie des Chalcidiens. *Compt. Rend. Acad. Sci. Paris.* Tom. cxiv. 1892. (Translated in *Ann. Nat. Hist.* (6). Vol. x.)

XIII. Heymons, R. Die Embryonalentwicklung von Dermapteren und Orthopteren unter besonderer Berücksichtigung der Keimblätterbildung. Monographisch bearbeitet. *Jena*, 1895.

XIV. Heymons, R. Die Entwicklung der weiblichen Geschlechtorgane von Phyllodromia germanica. *Zeitschr. f. Wiss. Zool.* Bd. liii. 1897.

XV. Heymons, R. Die Fortpflanzung der Ohrwürmer. *Sitzungsber. Akad. Wiss. Berlin.* 1894.

XVI. Heymons, R. Entwicklungsgeschichte untersuchungen an Lepisma saccharina. *Zeitschr. f. Wiss. Zool.* Bd. lxii. 1897.

XVII. Heymons, R. Flügelbildung bei der Larve von Tenebrio molitor. *Sitzungsber. Ges. naturf. Berlin.* 1896.

XVIII. Heymons, R. Grundzüge der Entwicklung und der Körperbaues von Odonaten und Ephemeriden. *Abh. Akad. Berlin.* 1896.

XIX. Heymons, R. Ueber die Bildung der Keimblätter bei den Insekten. *Mit. Akad. Berlin.* 1894.

XX. Heymons, R. Ueber die Bildung und den Bau des Darmkanal bei niederen Insekten. *Sitzungsber. Ges. naturf. Berlin.* 1897.

XXI. Heymons, R. Ueber die Fortflanzung und Entwicklungsgeschichte der Ephemera vulgata. *Sitzungsber. Ges. naturf. Berlin.* 1896.

XXII. Heymons, R. Zur Morphologie der Abdominalanhänge bei den Insekten. *Morph. Jahrb.* Bd. xxiv. 1896. And *Biol. Centralbl.* Bd. xvi. 1897.

XXIII. Hyatt, A., and Arms, J. M. The meaning of Metamorphosis. *Nat. Sci.* Vol. viii. 1896.

XXIV. Karawaiew, W. Die Nachembryonale Entwicklung von Lasius flavus. *Zeitschr. f. Wiss. Zool.* Bd. lxiv. 1898.

XXV. Knowa, H. The development of a Termite. *Johns Hopkins Univ. Circ.* Vol. xv. And *Ann. Nat. Hist.* (6). Vol. xviii.

XXVI. Korotneff, A. Zur Entwicklung der Mitteldarmes bei den Arthropoden. *Biol. Centralbl.* Bd. xiv.

XXVII. Krassilstschik, J. Zur Entwicklungsgeschichte der Phytophthires. Ueber Viviparität mit geschlechtlicher Fortpflanzung bei den Cocciden. *Zool. Anz.* Jahrg. xvi.

XXVIII. Kulagin, N. Beiträge zur Kenntniss der Entwicklungsgeschichte von Platygaster. *Zeitschr. f. Wiss. Zool.* Bd. lxiii. 1897.

XXIX. Lécaillon, A. Recherches sur l'œuf et sur le développement embryonnaire de quelques Chrysomélides. *Thèses présentées à la Faculté des Sciences de Paris.* Sér. A. 1898. Also *Zool. Centralbl.* Bd. v. 1898.

XXX. Lemoine, V. Étude comparée du developpement de l'œuf chez Puceron vivipare et ovipare. *Bull. Soc. ent. France.* 1893.

XXXI. Lemoine, V. Étude comparée du developpement de l'œuf dans la forme agame aptère dans la forme agame ailée et dans la forme sexuée du Phylloxera. *Zool. Anz.* Jahrg. xvi., pp. 140–142 and 145–149.

XXXII. Lemoine, V. Note complémentaire sur l'œuf du Phylloxera agame aptère. *T. c.* pp. 247 and 248.

XXXIII. Marchal, P. La dissociation de l'œuf en un grand nombre d'individus distincts et le cycle évolutif chez l'Encyrtus. *Compt. Rend. Acad. Sci. Paris.* Tom. cxxvi. 1898.

XXXIV. Möbusz, A. Ueber den Darmkanal der Anthrenus-Larve nebst Bemerkungen zur Epithelregeneration. *Archiv. f. Naturges.* Jahrg. lxiii. 1897.

XXXV. Nussbaum, M. Zur Parthenogenese bei den Schmetterlingen. *Archiv. f. Mikro. Anat.* Bd. liii. 1898.

XXXVI. Petrunkewitsch, A. Ueber die Entwicklung des Herzen bei Agelastica alni. *Zool. Anz.* Jahrg. xxi. 1898.

XXXVII. Rengel, C. Ueber die Veränderungen des Darmepithels bei Tenebris molitor während der Metamorphose. *Zeitschr. f. Wiss. Zool.* lxii. 1897.

XXXVIII. Saint-Hilaire, K. K. On the formation of the egg in Dytiscus. *Compt. Rend. Soc. St. Petersb.* 1895. (Russian, with résumé in German: Ueber die Enstehung des Eies bei Dytiscus.)

XXXIX. Tichomirow, A. Aus der Entwicklungsgeschichte der Insecten. *Festschr. Leuckart.* 1894. pp. 337–346.

XL. Uzel, H. Beiträge zur Entwicklungsgeschichte von Campodea staphylinus. *Zool. Anz.* Jahrg. xx. 1897.

XLI. Verson, E., and Bisson, E. Die postembryonale Entwicklung der Ausführungsgänge und der Nebendrüsen beim männlichen Geschlechtsapparat von Bombyx mori. *Zeitschr. f. Wiss. Zool.* Bd. lxi., pp. 318–337.

XLII. Verson, E., and Bisson, E. Die postembryonale Entwicklung der Ausführungsgänge und der Nebendrüsen beim weiblichen Geschlechtsapparat von Bombyx mori. *T. c.* pp. 660–694.

XLIII. Viallanes, H. Sur quelques points de l'Histoire du Développement Embryonnaire de la Mantis Religiosa. *Ann. Sci. Nat.* (7). Tom. xi. 1891.

XLIV. Wheeler, W. M. A contribution to Insect Embryology. *Journ. Morph.* Vol. viii. 1893.

XLV. Willey, A. Trophoblast and Serosa. A contribution to the morphology of the embryonic membranes of Insects. *Quart. Journ. Micro. Sci.* Vol. xli. 1899.

CHAPTER XXVIII.

GENERAL CONSIDERATIONS ON THE ARTHROPODA.

In reviewing once more the ontogeny of the various divisions of the Arthropoda, we are specially struck by the *uniformity of character* found among them. In the constitution of the eggs in the cleavage, the method of formation of the germ-layers and the shape of the embryo, there are so many points of resemblance that we are justified by ontogeny in regarding the Arthropoda as phyletically distinct, *i.e.*, as forming a natural group, even though, as will be shown below, the common stock divides near its root and gives rise to three great branches known to us under the names of the Crustacea, the Arachnida and the Myriopoda-Insecta.*

The eggs of the Arthropoda are as a rule distinguished by the *large quantity of yolk contained in them*, and the equal distribution of the latter (centrolecithal eggs of the Arthropoda). The typical method of cleavage in the Arthropoda is a *superficial one*, which has developed from total and equal cleavage, as may be seen from the ontogeny of various Crustacea.† We also see that the Arthropodan eggs, in those cases in which the food-yolk has secondarily degenerated, undergo total cleavage (Clacodera, *Peripatus Edwardsii*,‡ parasitic Insects). In other cases the total cleavage perhaps still represents a primitive condition, *e.g.*, in *Branchipus*. In a few Arthropoda, the egg appears to be telolecithal, and the cleavage is at first restricted to only a small part of the egg (*e.g.*, in *Mysis*, *Cuma*, some Isopoda, and the Scorpiones). This apparently different method of cleavage is, however, to be traced back to superficial cleavage.

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* [See *Natural Science*, Vol. x. "Are the Arthropoda a Natural Group?"—Ed.]

† The statements in this chapter are based upon the facts already given in connection with the different divisions of the Arthropoda. The reader must refer for these to the preceding chapters.

‡ [See footnote, p. 165.—Ed.]

Superficial cleavage, as a rule, occurs only in the Arthropoda. Where other forms, *e.g.*, *Renilla*, *Clavularia* (Vol. i., p. 76) show a similar method in the first stages, this does not lead to the same results as typical superficial cleavage, viz., to a unilaminar blastoderm covering the whole surface of the egg with a uniform layer and an accumulation of food-yolk filling the cleavage-cavity.*

The **formation of the germ-layers** is introduced by gastrulation, which, in many cases, is of the invagination-type (*Moina*, *Lucifer*, *Astacus*, *Peripatus*, *Hydrophilus*), in others, on the contrary, gastrulation is replaced by a solid ingrowth of cells (*Ligia*, *Limulus*, Scorpiones, Araneae, Myriopoda). The position of the blastopore varies in the different groups. As a rule, the blastopore corresponds to the ventral side of the body.

In *Peripatus* and the Insecta, the blastopore is an exceedingly long slit, the anterior end of which corresponds in position to the mouth, and the posterior end to the anus (Figs. 99, 134, and 145). In the Crustacea, on the contrary, the blastopore is said to belong to the posterior end of the germ-band, and to correspond more or less in position with the later anal aperture. The accounts given of the Arachnida seem to indicate that, in position, the blastopore may be related to the anus.

The act of gastrulation leads to the breaking up of the common rudiment of the entoderm and the mesoderm. The rudiment of the mesoderm in the Arthropoda is always multicellular, except perhaps in a few quite isolated cases, such as *Cetochilus*. In the Insecta, the formation of the mesoderm may be traced back to a folding of the lateral diverticula of the archenteron (Figs. 154 and 155, p. 314). The processes that take place in *Peripatus* may perhaps be interpreted in the same way, although in this form we are inclined to assume, in agreement with the Annelida, the development of two mesoderm-bands advancing from behind forward through the multiplication of cells. The facts as yet known of *Peripatus* seem rather to support this last view. The question whether the condition found in the Insecta (*i.e.*, the rise of the mesoderm from the archenteron through folding) represents a primitive or a derived condition, is connected with the as yet unsolved problem of the first (phylogenetic) rise of the mesoderm.

In the Crustacea, the mesoderm arises in the form of a growth at the lips of the blastopore. The same is most probably the case in

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* [For a comparison of the cleavage and formation of the germ-layers in the Arthropoda, see WAGNER (No. X.).—ED.]

the Arachnida. In the latter, the mesoderm runs forward from the point of origin in the form of two bands (mesoderm-bands) on either side of the middle line. These two bands are also found in *Peripatus*, the Myriopoda, and the Insecta, as well as apparently in the Pantopoda, while, in the Crustacea, the arrangement of the mesoderm is less regular. Some Crustacea, however (*Branchipus*, *Cymothoë*), show a similar regular form of mesoderm-rudiment.

The paired rudiment of the mesoderm breaks up into segmental divisions in a somewhat similar way in all Arthropoda. These divisions are the primitive segments (mesodermal somites), which either become hollow, and are then known as coelomic sacs, or are not thus modified, but soon break up into mesenchymatous tissue. This latter is the case in most Crustacea, in which coelomic sacs are rarely to be found, but the former condition occurs in the Xiphosura, Arachnida, Pantopoda, Onychophora, Myriopoda, and Insecta.

Although the primitive segments have as a rule a very similar fate, and undergo similar modifications in all Arthropoda, certain differences are to be found in the various classes in the size attained by them, and in the time at which their further differentiation begins. The most primitive condition is exhibited in *Peripatus*, in which the primitive segments in their large size resemble those of the Annelida (Fig. 100, p. 200). The Myriopoda and the Orthoptera follow next in the conspicuous development of the primitive segments within the germ-band (Figs. 168 and 169 *A*, p. 343), while in the other Insecta the coelomic sacs are from the first small, a considerable part of the mesoderm being, as a rule, excluded from participation in the formation of these sacs (Fig. 158, p. 321). In the Crustacea, the development of the coelomic sacs is almost entirely suppressed. The Arachnida, on the contrary, which in many other respects appear as a modified group, are distinguished by the fact that in them the coelomic sacs are unusually large, and even in the later stages of embryonic development (at the time when the heart is forming) extend almost to the dorsal middle line (Fig. 45 and 46, p. 88).

The **appearance and further development of the organs** in the different groups of the Arthropoda show remarkable and important agreement.

In the case of the **nervous system** it has been proved that an invaginate middle strand and two lateral strands almost universally take part in the formation of the ventral chain of ganglia. The fibrous substance appears on the inner surface of the ganglionic rudiments, and is only later taken into the latter, a process which must be regarded as specially primitive, and is to be found taking place in a somewhat similar manner in all the various groups.

While the formation of the chain of ganglia takes place, as a rule, by a process of delamination from temporary ectodermal grooves which afterwards vanish, permanent invaginations occur which take part in the formation of the brain, leading no doubt chiefly to the formation of the optic ganglia. The appearance of these more or less extensive depressions, known as cephalic pits, is specially characteristic of the various divisions of the Arthropoda (*Peripatus*, the Myriopoda, the Insecta, *Limulus*, the Arachnida). In *Peripatus*, indeed, another significance has been attributed to these depressions, and it is doubtful whether they participate in the formation of the brain. The depressions in the cephalic region in *Peripatus* correspond to similar pit-like invaginations arranged in pairs which recur in each of the trunk-segments. The nature of these remarkable structures, which are very characteristic of *Peripatus*, has not yet been established, but similar depressions have been described in the Myriopoda and the Pantopoda.

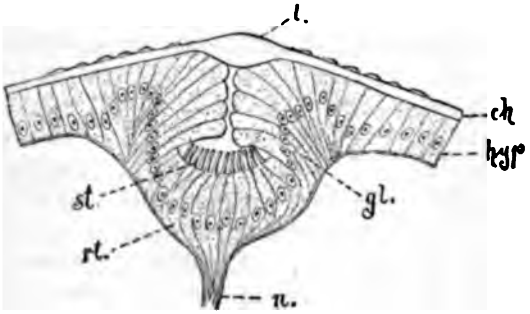

FIG. 195.—Section through the ocellus of a *Dytiscus* larva (after GRENACHER). *ch*, chitinous covering of the body; *gl*, vitreous body; *hyp*, hypodermis; *l*, lens; *n*, optic nerve; *rt*, retina; *st*, rods.

The development of the **eyes** may be closely connected with the cephalic pits just mentioned which, as it appears, chiefly give rise to the formation of the optic ganglia (Scorpiones, Araneae). However much the permanent Arthropod eyes vary with regard to structure, they may, in the first instance, be traced back to pit-like depressions of the ectoderm, and in explaining them we must start from such simple eyes as those occurring in the larvae of Insects and in many Myriopoda. This simplest form of Arthropodan eye, the ocellus (Fig. 195), consists of a depression of the hypodermis, the cells of which have become differentiated into the so-called vitreous body (*gl*), and retinal cells (*rt*), secreting rods. The unilaminar character of the hypodermis has, however, been retained in this simple eye, so that it appears as a mere continuation of the hypodermal layer (Fig. 195, *hyp*, *gl*, *rt*). Over the eye lies the lens which has arisen by the thickening of the outer chitinous covering of the body, and is secreted by the hypodermis (lentigen or vitreous body-layer). From such a simply constructed eye we have to derive the complicated eyes found among the Arthropoda, but in so doing we must distinguish sharply between the various phyletic ontogenetic series of the Arthropoda, and we must remember that it is not possible to regard as directly related one to another the various forms of compound eyes found in the separate divisions such as the Crustacea and the Insecta, although the eyes in these groups are very similar in structure.

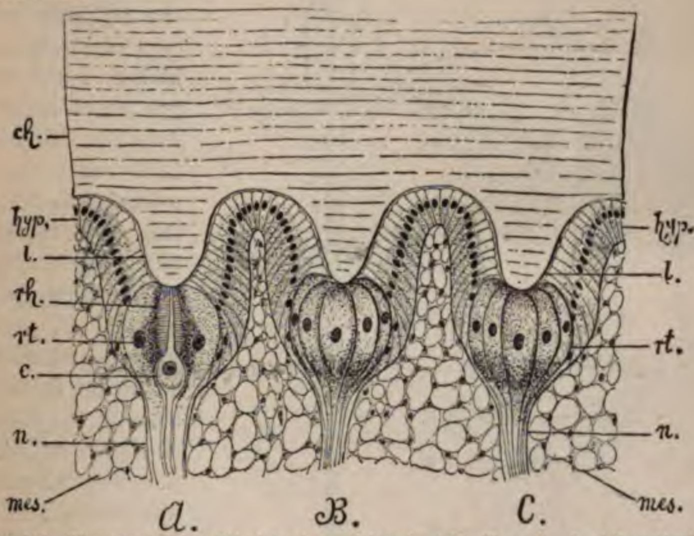

FIG. 196.—Three ommatidia of the lateral eye of *Limulus* (after WATASE). In *A* the retinula is supposed to be cut through medianly, in *B* and *C* it is retained whole. *c*, central ganglion-cells; *ch*, chitinous covering; *hyp*, hypodermis; *l*, lenticular sphere; *mes*, mesodermal tissue; *n*, nerve; *rh*, rhabdom; *rt*, retinula.

It may appear at first sight unreasonable not to regard the compound eyes of the Crustacea and the Insecta, which are so remarkably similar in organisation, as directly related one to the other, but when the phylogenetic course of development of the two divisions is taken into account we shall have to take up this position. It can only be assumed that the development of compound eyes is a character of the Arthropodan organisation, and that it takes place in the different divisions (Crustacea, Arachnida, Myriopoda, and Insecta) independently, and yet may lead, as in the Crustacea and the Insecta, to almost the same result.

The eyes of *Peripatus* differ altogether in structure from those of other Arthropoda. The eyes of this form also, indeed, originate as depressions, which, however, close to form vesicles and become separated from the hypodermis. The lens is secreted within the optic vesicle. The eyes of *Peripatus* thus, in their ontogeny, pass through the stage of the simplest Arthropod eye, but then rise to a higher level than that attained by the latter, and can far better be compared with the higher forms of eye found in the Annelida. In any case, we do not recognise in them the Arthropodan type of eye.

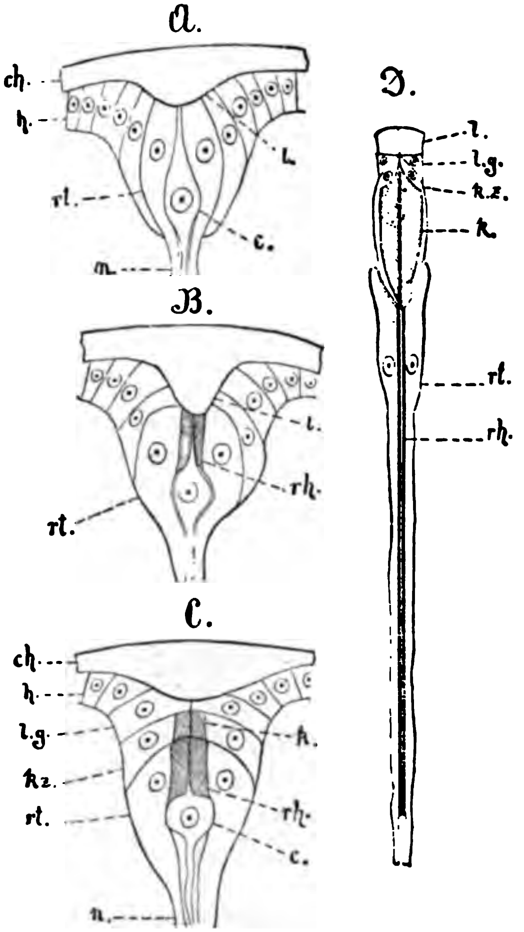

Fig. 197.—*A*-*D*, diagrams illustrating the development of an ommatidium from a depression of the hypodermis. *D* represents an ommatidium from the compound eye of an Amphipod (*Talorchestia*, after Watase). *c*, central cell; *ch*, chitinous covering of the head; *h*, hypodermis; *k*, crystalline cone; *kz*, crystalline cone-cells; *l*, lens; *lg*, lentigen cells; *n*, nerve; *rh*, rhabdom; *rt*, retinula cells.

The *facet-eyes* of the Insecta must be regarded as arising from a massing together of simple ocelli in the way already indicated in the Myriopoda. The latter group, in the simplest cases, have only a few ocelli on each side (*Scolopendra* four), but their number may increase (*Lithobius*, *Julus*, thirty to forty on each side), and in some forms (*Scutigera*) there may even be as many as 200 ocelli on each side, which, by their close approximation, recall the appearance of facet-eyes, although a group of eyes does not possess the true structure of the latter. Each ocellus in this way becomes a single ommatidium of the facet-eye. The diminution in number of its elements which it then undergoes, and the simultaneous formation of the rhabdoms are consequences of the subordination and loss of individuality of the originally distinct single eyes on becoming merged in the complex eye, of which organ they now form a part.

Attempts have been made to trace back the facet-eye to the more primitive form from which it originated, by regarding the ommatidia which, according to the view mentioned above, were derived from single ocelli, as simple hypodermal depressions which, in consequence of the length of the ommatidia, became very deep (Fig. 197 *D*). In making such an attempt to explain the structure of the ommatidia it is best to start from a depression of the hypodermis which corresponds to a simplified ocellus (Fig. 197 *A*). As the depression deepens and, instead of rods, rhabdoms begin to form in the retinal cells, this eye reaches a grade of development (Fig. 197 *B*) essentially equivalent to that of an ommatidium in the lateral eyes of *Limulus* (Fig. 196). The lateral eye of *Limulus* is composed of a number of single eyes formed of only a few cells (Fig. 196). These unilaminar eyes are quite continuous with the hypodermis, but already show rhabdom-formation (Fig. 196 *A*, *rh*). It is indeed not certain whether the eyes of *Limulus* should really be regarded as primitive eyes, or as degenerate forms of the compound eye; in any case, however, we can imagine that the higher facet-eyes passed through a similar stage (Fig. 197 *B*).

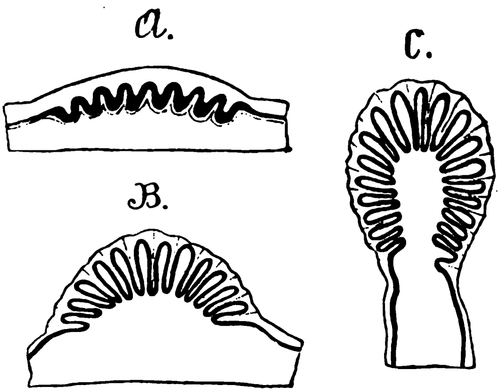

FIG. 198.—Diagrams illustrating compound eyes in longitudinal section. *A*, Limulus; *B*, a larva of *Agrion*; *C*, *Branchipus* (after WATASE). The thick black line represents the hypodermis, and each of the depressions formed in it represents an ommatidium.

When the depression deepens, another series of hypodermal cells may be drawn into the formation of the eye (Fig. 197 *C*), these representing the crystalline cone-cells (*kz*) of the ommatidium. A series of lentigen cells may also be utilised in the formation of the eye (Fig. 197 *C*, *l.g*). The further deepening of the optic pit, and the great lengthening of the cells lead finally to the form of the ommatidium (Fig. 197 *D*). The hypodermal cells, the lentigen cells, the crystalline cone-cells, and the retinal cells thus appear as a *unilaminar layer* of long cells penetrating far down, and having the same arrangement as in the simple ocellus (Fig. 195). The lumen here, however, is not open as in the ocellus, but filled by the mass of the crystalline cone and rhabdoms, but this does not constitute an essential difference between the two eyes. The grouping together in larger or smaller numbers of these single eyes which arise as simple depressions of the hypodermis is elucidated by Fig. 198, which at the same time represents the arrangement of the ommatidia on a convex base usual in most facet-eyes, and determined by the functional requirements of the eye.

The method of composition of the facet-eye here described is essentially in keeping with the view long ago maintained by GRENACHER. This author starts from a simple eye consisting of few elements, such as is represented by an ommatidium of an acone facet-eye of the *Tipulidae*, and derives the facet-eye through the increase in number of these eyes, and the ocellus through the multiplication of the elements with the retention of the single lens. In the simple eye, which here forms the starting-point, we have an ocellus of specially simple structure.

It has already been stated that the *compound eye of the Crustacea* must be regarded as belonging to another ontogenetic series. It will therefore not be a matter of surprise to find that it deviates in many ways from the above in its development. The character of the compound eye is, in the Crustacea, always preserved. In some cases, *e.g.*, in the Isopoda, it might appear as if we had before us transition stages between the simple and the compound eye, but it is more than probable that, in this branch of the Crustacea, we have to do merely with a simplified form of the facet-eye.

This view of the Isopodan eye was adopted long ago by GRENACHER, who attempted to solve the question as to how the very simple eye of the Isopoda was related to other Arthropodan eyes, by maintaining that the former was to be regarded as a compound eye in consequence of its possessing a double crystalline cone and a retinula forming rhabdoms and divided into seven parts. It cannot therefore be doubted that, in the Isopodan eye, which is not unlike a group of single eyes, we have a secondary form, and this is in itself very probable, inasmuch as the Isopoda are, in many respects, a highly modified group of the Crustacea. A degeneration of the facet-eye, which was originally stalked in the Malacostraca, has taken place in any case in this order.

We have no indication of the manner in which the facet-eye has arisen in the series of the Crustacea. None the less must we consider that this eye, which closely resembles the facet-eyes of the Insecta, arose in the same way as the latter. Any deviations that may occur, such as the presence of another cell-layer in the ommatidium (Fig. 197 *D*, *l.g*), are to be explained simply by the inclusion of another row of cells in the hypodermal depression, as already shown.

The structure, development, and relations of the unpaired median eyes in the Crustacea are still little understood. It has recently been asserted that they arise by inversion (CLAUS, No. 3), and since this method of formation is characteristic of some of the eyes found in *Limulus* and the Arachnida, relations between the median Crustacean eye and the median eye of *Limulus* and the Scorpiones, as well as the so-called principal eyes of the Araneae, are suggested.

The *eyes of the Arachnida* belong to a third ontogenetic series. They have only one lens, and are thus devoid of the characteristic feature of facet-eyes, but in the eyes of *Scorpio* we find a grouping of the cells into retinulae and the formation of rhabdoms within these latter, and in this respect they may claim to be compound eyes. We considered ourselves justified in explaining the common lens as having arisen by the flowing together of distinct corneal lenses (p. 71, etc.), and find in the lateral eyes of *Limulus*, which also show rhabdom-formation, an indication of such a fusing of the lenses. We tried further to show it to be probable that the eyes of the Araneae, which in their present form appear to be simple eyes, are to be derived from compound eyes, this origin being still indicated in their development and their structure. It is highly probable also that the compound eyes of the Arachnida, like those of the Insecta, arose through the accumulation of simple hypodermal depressions resembling ocelli.

When we turn to the ontogenetic formation of the Arthropod eyes, we find that the simple forms arise as pit-like depressions of the ectoderm. In the higher forms, *i.e.*, in the compound eyes, this primitive method of formation is obliterated. The single eyes here arise merely through the differentiation of a cell-layer without special depressions. Where such a depression is found in the development of a compound eye, it leads to the formation of the eye as one whole. In this last process, as in the differentiation of the single eyes out of a multilaminar cell-layer, we have secondary phenomena representing a simplified method of formation of the compound eye. It should also be noted that the ontogeny of the Arthropod eye is as yet not satisfactorily explained.

The **respiratory organs** of the Arthropoda must be dealt with separately, according to the different phylogenetic series into which they are to be divided. Since we derive the Arthropoda from forms which live in water, it appears to us that the most primitive form of respiratory organ must have been a tubular or leaf-like outgrowth of the body-surface. Such a simple form of respiratory organ is found in the gills met with as branchial tubes in the Annelida and Crustacea. These branchial structures appear, as a rule, as appendages of the extremities. The gills of *Limulus* are also leaf-like appendages of the abdominal limbs. From these we have to derive the lung-sacs of the Arachnida (Scorpiones, Araneae), a fact indicated by the method of development of these latter. In the transformation of gills into lungs we recognise an adaptation to life on land. When this adaptation goes further, it leads to the development of unbranched tracheal tufts (Araneae) which finally ramify in a dendriform manner and develop a spiral filament (Pseudoscorpiones, Solifugae). In this way is attained the same type of tracheal system as is produced in different manner in other groups of Arthropods otherwise very far removed from the above, viz., *Peripatus*, the Myriopoda, and the Insecta. In the forms which were the starting-point of this last series, the tracheae appeared as depressions of the body-surface, which at first were irregularly distributed over the body (*Peripatus*), but later attained to definite segmental arrangement. The tracheae in the Myriopoda and the Insecta arose as such segmentally-arranged depressions. The branches of the tracheal system are formed by the splitting and branching of the original invaginations. In the Insecta these tracheal rudiments appear very early, in the Myriopoda, on the contrary, much later, and, as *Peripatus* in this way resembles the Myriopoda, this late appearance of the tracheal rudiments has been regarded as an indication of their having been recently acquired. The similarity in structure between the tracheae of the Arachnida and those of the Myriopoda and Insecta is remarkable. The presence of the spiral filament in these two forms of tracheae, which must be regarded as having arisen independently in the two groups, is specially striking, but this feature loses its value as an indication of a common origin when it is seen that such a spiral thread also occurs in other tubes lined by a chitinous intima, *e.g.*, the efferent ducts of glands (salivary and spinning glands of the Insecta) and the vas deferens of the *Cytheridae*, p. 335).

The so-called closed tracheal system of many aquatic larvae, *e.g.*, those of the *Ephemeridae*, as well as the tracheal gills connected with it, are to be regarded as a form of respiratory organ secondarily acquired in adaptation to life in water.

The **fore- and hind-guts** arise in the Arthropoda as ectodermal invaginations, the stomodaeum and the proctodaeum. The excretory tubes known as Malpighian vessels found in the Myriopoda and Insecta are diverticula of the proctodaeum. The same name is given to similar blind tubular appendages of the intestine in the Arachnida, but, since ontogeny makes it probable that the latter belong to the enteron and are thus not of ectodermal but of entodermal nature, they ought not to be homologised with the Malpighian vessels. Tubular appendages similar in structure and function are, on the other hand, found at the end of the enteron in the Crustacea (Amphipoda), but these most probably must be regarded merely as analogous structures.

The phylogenetic origin of the Malpighian vessels is still obscure. It has been thought that they might be true nephridia, which have become connected with the proctodaeum, since structures resembling the nephridia are in some Annelids found connected with the intestine (Nos. 2 and 9). In one case, that of the *Megascolides* examined by SPENCER, these glandular tubes, which in structure are extraordinarily like nephridia, are, indeed, connected with the stomodaeum, while, in *Acanthodrilus*, BEDDARD found similar structures connected with the proctodaeum. Just as, in *Peripatus*, nephridia have been found drawn into the buccal cavity as salivary glands, so we might suppose nephridia drawn into the proctodaeum, a process which is perhaps more probable *a priori* than the former, since the nephridia in this case retain their original function. Against such a view we have the ectodermal or entodermal origin of these excretory tubes, and this is of all the greater weight since, according to recent researches, the nephridia arise altogether from the mesoderm, and it would therefore be impossible to imagine a persistence and a specially strong development of the ectodermal portion simultaneously with a complete degeneration of the mesodermal (inner) section.*

The formation of excretory tubes starting from the intestine, such as has been observed in the Amphipoda, is a noteworthy indication of the fact that parts of the intestine are capable of taking over the function formerly carried on by the nephridia. Even in the *Nauplius* we find a part of the intestine utilised for excretion, the cells filled with urinary concretion forming slight swellings (Vol. ii., Fig. 89, *ds*, p. 191). When these parts are transformed into caeca or lengthen out like tubes, we have the excretory tubes of the Amphipoda (eventually also of the Arachnida) or the Malpighian vessels of the Myriopoda and Insecta, according as, in each case, the process takes place in the enteron or

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* [Some recent observers (GOODRICH, *Quart. Journ. Micro. Sci.*, Vol. XXXVII., 1895, and MEISSENHEIMER, *Zeitschr. f. Wiss. Zool.*, Bd. lxiii., 1898), suggest that the primitive nephridia may be largely if not wholly ectodermal, and would distinguish these from the genital ducts and certain secondary nephridia, which arise from the mesoderm as coelomic funnels.—ED.]

the proctodaeum. We are therefore far more inclined to regard the Malpighian vessels as new structures coming into use on the degeneration of the nephridia, than to trace them back to the actual nephridia.

The **development of the enteron** is essentially influenced by the relations of the entoderm-rudiment to the mass of the food-yolk. The latter, which originally fills the cleavage-cavity, is taken up later into the enteron. This process may take place in various ways: (1) the yolk may filter through the wall of the enteric sac (*Astacus*), or (2) the entoderm-cells may wander through the yolk to constitute the enteric epithelium at its surface (Crustacea, *Limulus*, Araneae, Chilopoda), or finally (3) the food-yolk may be grown round by the entoderm-rudiment (*Mysis*, Isopoda, Scorpiones (?) Insecta). The formation of the intestinal epithelium in some cases only takes place very late (Araneae), and then the splanchnic layer of the mesoderm, which has meanwhile developed, becomes closely applied to the yolk-mass. Septa-like processes then grow out from it into the yolk-mass and isolate single complexes of the latter, which appear like diverticula. As in the central part of the enteron, so also in these diverticula, the formation of the epithelium only commences at a later period. The diverticula represent the rudiments of the hepatic lobes, which, in the Crustacea, are formed in the same way, the only distinction being that, in the latter, the differentiation of the epithelium takes place much earlier.

Since, in some Arthropoda, only a part of the food-yolk is taken up into the interior of the intestine, it may happen that smaller or greater masses of yolk remain behind in the body-cavity and there undergo a gradual absorption (*Moina*, *Mysis*, and the Dipterous Insects). In the Diplopoda, this condition, which elsewhere is exceptional, appears developed to a high degree, for here the enteron is said to arise as a somewhat narrow tube in the middle of the yolk-mass. As a consequence of this, the greater part of the yolk would come to lie in the body-cavity. Here, as in the Crustacea above mentioned, the yolk-mass in the body-cavity is thickly surrounded and interpenetrated by mesoderm-cells.

We must next consider the **development of the mesoderm**. The coelomic cavities of the primitive segments, which, in some cases (*Peripatus* and the Arachnida), have been seen to attain such high development, do not, in the Arthropoda, become the definitive body-cavity, but sooner or later the primitive segments undergo degeneration. But before this occurs, the formation of the heart starts from the primitive segments, single cells of the coelomic sacs of the two sides becoming detached and uniting to form the dorsal tube. The primitive segments then break up to some extent, single cells from various parts wandering into the primary body-cavity and there forming a kind of mesenchyme. The permanent body-cavity arises through the appearance of lacunae in this mesenchyme and the flowing together of these lacunae to form large spaces. As a last remains of the primitive segments we have the pericardial septum so characteristic of the Arthropoda which cuts off a dorsal part of the body-cavity surrounding the heart (the pericardial space) from the larger ventral portion.

Besides the parts just mentioned, the primitive segments yield the formative material for the nephridia. In *Peripatus*, where the nephridia appear, as in the Annelida, in all the trunk-segments, a considerable portion of the primitive segments is directly utilised for the formation of the nephridia. In the other groups, the whole question of the rise of the organs known as nephridia is still undecided, but it may be mentioned as very probable that the salivary glands and anal glands of *Peripatus*, the antennal and shell-glands of the Crustacea, the coxal glands of *Limulus* and the Arachnida, as well as the efferent genital ducts, are derived from nephridia, and in any case are mesodermal in origin. The nephridial nature of the organs of *Peripatus* just mentioned, and of the antennal and shell-glands of the Crustacea, may be regarded with some certainty as definitely established. The aperture of the efferent genital ducts varies greatly in position in the different divisions of the Arthropoda. From this we may conclude that, in the different cases, the nephridia of different segments have been drawn into the formation of the genital ducts (Chilopoda and Diplopoda), although, in some cases, the idea of a secondary shifting of the opening through several segments is suggested. (In the Insecta, the apertures of the genital organs vary from the seventh to the ninth segment. In the *Ephemeridae*, the female genital aperture is found on the seventh segment, while, in other Insects, it lies behind the eighth segment.)

The *genital glands* also are derived from the primitive segments, these being found as growths of the epithelium of the coelomic sacs, and thus having an origin exactly similar to that of the genital glands of the Annelida (Vol. i., p. 297). A further agreement with the Annelida is found in the fact that the remains of the coelomic sacs may pass direct into the cavity of the genital gland, so that the genital products budding off from the peritoneal epithelium can still fall into the secondary body-cavity (coelomic or genital cavity), and pass out from there through the efferent (nephridial) ducts (*Peripatus*, Myriopoda). The whole of that part of the primitive segments that is utilised for the formation of the genital glands fuses with those pairs of primitive segments which yield the efferent ducts (nephridia of the genital segments), the continuity between the genital glands and ducts being thus attained. In the Crustacea, as well as in the Arachnida and in the Insecta, there are secondary conditions of development of the genital organs, which, however, are to be traced back to the more primitive conditions just described that still occur in *Peripatus* and the Myriopoda.

In consequence of the great abundance of food-yolk in the eggs of the Arthropoda, only the ventral side of the embryo at first appears in the form of a **germ-band**; to this rule, however, there are frequent exceptions. The eggs, as has been mentioned, are occasionally small and have less yolk, which may be (in certain rare cases) traceable to a primitive condition, but in most cases must be regarded as a secondary phenomenon. In these cases, the spherical form of the egg may pass directly into the definitive shape of body.

The germ-band which, in different forms, occupies a more or less considerable part of the egg, arises partly by the ectoderm-cells on the ventral side of the egg becoming elongated, partly by the appearance beneath it of the two other germ-layers, especially of the mesoderm-bands. Besides this, the band-like thickenings of the ectoderm soon appear near the ventral middle line, representing the rudiment of the ventral chain of ganglia, which, indeed, very soon breaks up into segments. A much widened anterior section of the germ-band very soon becomes distinguished from the primary trunk of the embryo as the cephalic lobes. The trunk soon breaks up into segments, this modification chiefly involving the mesoderm (formation of the primitive segments), but may also be indicated on the external surface of the germ-band even before the appearance of the primitive segments (*Hydrophilus*, *Chalicodoma*). The series of limb-rudiments appear as outgrowths of the surface on each side; in most Arthropoda, a process of a coelomic sac passes into each of these limbs, so that they at first appear hollow (*Peripatus*, Myriopoda, Orthoptera, Arachnida, Pantopoda). Even in those forms which, in the adult, have no limbs on the abdomen (Arachnida, Insecta), abdominal limbs are found in the embryo; the abdomen of the embryo also may consist of a larger number of segments than that of the adult (Araneae), an indication of the fact that these forms are descended from ancestors which possessed a richer segmentation of the body and a larger number of appendages.

The germ-band does not always retain its primitive position on the surface of the egg, but may shift into the interior by undergoing a ventral curvature (Myriopoda), or else, by the development of special **embryonic envelopes** (*amnion* and *serosa* of the Insecta), it may sink more deeply beneath the surface of the egg. A similar but merely analogous development of embryonic envelopes is only found among other Arthropoda in a few viviparous forms (*Scorpio* and *Peripatus Edwardsii*). [*Cf.* App. Lit. Insecta, Nos. XVI. and XLV.]

The germ-band which until now corresponded merely to the ventral portion of the embryo, spreads out over the lateral and dorsal parts of the yolk which, so far, were only covered by a thin layer of cells, these being now involved in the further shaping of the embryo, the dorsal surface of which is thus produced. In the Insecta, these last processes of development become complicated by the process of the involution of the embryonic envelopes which takes place simultaneously. The closure of the dorsal body-wall completes the external development of the embryo, which, after corresponding further development of its internal organs, is ready for hatching.

The newly-hatched embryo either resembles the adult, or else differs from the latter, in which case it passes through a more or less complicated **metamorphosis**. The process of metamorphosis differs greatly in character in the different groups of the Arthropoda, but must in all cases be regarded as the development of secondarily acquired larval stages (Crustacea, Pantopoda, Insecta). The hatching embryo either consists of merely a few segments (Crustacea, Pantopoda) and only acquires the complete number of segments during the course of metamorphosis (Diplopoda), or else has the full number of segments as well as of body-regions possessed by the adult, from which it is distinguished only by its different manner of life and by deviations in the shape of the body determined by this life (Insecta). We find, for instance, that wings are wanting in all the larvae and young forms of Insects, this characteristic of the most highly developed Arthropods being thus proved to be a comparatively late acquisition, a view which is confirmed by the fact that wings are still altogether wanting in the lowest Insects (Apterygogenea, p. 260).

One of the special characteristics of the metamorphosis of the Arthropoda is the series of consecutive different larval stages which pass one into the other through *processes of ecdysis*. Such moults may also occur during embryonic life, and are even often found at an extraordinarily early period before the germ-band has appeared (*blastodermic cuticle* of the Crustacea), or else before the limbs have formed (*embryonic cuticular envelope* of *Limulus*, *deutovum-membrane* of the Acarina, embryonic envelopes of *Pentastomum*). All these cuticular envelopes then form a further covering to the embryo within the egg-integument.

Zoologists were for a long time inclined to ascribe to the larvae of the Arthropoda an important phylogenetic significance. But when it was recognised that these larvae often represented secondarily modified (adapted) forms (*Nauplius*, *Zoaea*, *Pantopodan larva*, *caterpillar of Insects*), the comparison of the adult forms received more attention, a far higher value being set upon this branch of inquiry. The recent advance in the knowledge of *Peripatus* has been of special significance in *interpreting the Arthropoda, and in tracing them back to lower forms*. Too great importance was indeed attached to those characters of *Peripatus* that pointed to the Annelida, and gave rise to doubt as to the uniformity of the Arthropod stock.* As it was seen that the Myriopoda and the Insecta could be linked on directly to the Annelida through *Peripatus*, the only way out of the difficulty caused by the Crustacea, which were apparently far removed from *Peripatus* and in some respects showed less primitive conditions, was to assume for them an independent origin for the Annelidan stock. Recent research has, however, made it appear that *Peripatus* is more closely related to the Arthropoda than was formerly assumed. The nephridia are closed by end-sacs (remains of the coelom), and show the type which we find recurring in the antennal and shell-glands of the Crustacea. The permanent body-cavity is a pseudocoele which develops after the disintegration of the coelomic sacs through the enlargement of the primary body-cavity. The heart is of the

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* Doubts of this kind have repeatedly been expressed. They have found an able exponent in the anonymous author of an article in *Kosmos* (No. 1), who argues against the unity of the Arthropodan stock. OUDEMANS, in the same way, is in favour of breaking up the division of the "so-called Arthropoda" (No. 8), and FERNALD, in his recent treatise on the "Relationships of the Arthropoda" (No. 4), gives indications of holding a similar view. This latter author, indeed, derives the three great principal trunks of the Arthropodan stock, the Crustacea, Arachnida, and Insecta, from a common root. This root, however, does not spring from the Annelida, but reaches back to the unsegmented forms from which also the Annelida are derived, though in another direction. *Peripatus* then branches off, and thus is not directly connected with the three great branches of the Arthropodan stock, the Myriopoda also being independent of these. These latter are, however, thought by FERNALD to be connected with *Peripatus*. In any case the complete uniformity of the Arthropodan stock is not held by these authors, and it is also opposed by KINGSLEY (No. 7), who, in spite of their many points of agreement, derives the Crustacea and the Insecta from different starting-points. [See also No. XII.—ED.]

type which is universal among the Arthropoda—a dorsal vessel with lateral pairs of ostia. The development of *Peripatus* also, for a knowledge of which we must start from the New Zealand form which unfortunately is too little understood, is linked on to that of other Arthropoda.* We have here in the first place an egg rich in yolk, with superficial cleavage. The characters in which *Peripatus* stands opposed to the Arthropoda are the position and constitution of the extremities which are not actually jointed (we leave out of account here the Tardigrada and *Pentastomum*, the relationships of which are uncertain), and especially the structure of the eyes, which must be regarded as an inheritance from Annelidan ancestors that was lost in other Arthropoda, and replaced by the ommateal eyes (ocelli and facet-eyes).

After what has been said above, we seem to be justified in assuming for all Arthropoda (*Peripatus* included) a common origin from the Annelidan stock. In giving the name Protostraca to the hypothetical racial form of the Arthropoda which proceeded from the Annelida, and for which very primitive characters must be assumed if it is to serve as the starting-point of all known classes of Arthropods, the fact is expressed that the Crustacea in certain features of their organisation, especially in structure of their limbs, which can be traced back to the biramose form of parapodium, have preserved, in consequence of their retention of a pelagic manner of life, primitive characters. On the other hand, the form of extremities found in *Peripatus* (and partly retained in the Palaeostraca†) must be considered as a secondary adaptation to a terrestrial existence.

Starting from the Protostraca, according to the present condition of our knowledge, we may, as has been already remarked, assume three great series of development of the Arthropodan stock, by the side of which a number of smaller independent branches have been retained. One of these series leads through the hypothetical primitive Phyllopod to the Crustacea; the second through the Palaeostraca to the Arachnida; the third through forms resembling *Peripatus* to the Myriopoda and the Insecta. The Pantopoda and the Tardigrada must probably be regarded as smaller, independent branches of the Arthropodan stock.

If we try briefly to enumerate the general characters in which the Arthropoda are to be distinguished from the Annelida, we must point first to the great development of the cuticular integument and the

* [See footnotes, pp. 165 and 216.—Ed.]

† [See Vol. ii., p. 333, footnote.—Ed.]

more ventral position of the limbs, some of which, as jaws, bite one against the other. This last point is of importance, because the jaws of the Annelida are mere cuticular secretions of the stomodaeum, and not appendages. We should mention further the degeneration of the coelomic sacs and of the nephridial system. The former undergo disintegration through the development of a secondary pseudocoele, and the latter, in the higher forms, through the acquisition of a new excretory apparatus. In direct connection with the condition of the body-cavity we have the absence of a closed blood-vascular system, and the development of that type of heart characteristic of the Arthropoda.

Another peculiarity recurring throughout the whole series of the Arthropoda is the enlargement of the primary cephalic region by the addition of originally post-oral segments. It might be worth while to attempt to attain a fixed point for the homologising of the anterior pair of limbs in the various Arthropoda, but in the present state of our knowledge such an attempt would have to be made with the greatest care. We may perhaps conclude from the segmentation of the brain, that the antennae of *Peripatus*, the Myriopoda, and the Insecta are homologous with the first antennae of the Crustacea. We should then perhaps be able to consider the jaws of *Peripatus*, which are included in the mouth, and the ganglion of which is approximated to the brain (in the same way as are the antennal ganglia of the Crustacea), as the equivalents of the second antennae of the Crustacea, which, indeed, in the *Nauplius* still function as masticatory organs. We are perhaps justified in assuming that, in the Myriopoda and Insecta, these extremities are completely lost, so that the mandibles of the Insecta (the homologues of the oral papillae of *Peripatus*), would then have to be related to the mandibles of the Crustacea. We might further assume that the chelicerae of the Arachnida correspond to the second antennae of the Crustacea, a view that is supported by the condition of their ganglia which fuse with the brain. The homologue of the first antennae would, in this case, be lost, but it is seen to reappear ontogenetically as a transitory structure (p. 111). The pedipalps would thus be the equivalent of the mandibles of the Crustacea and Insecta, whereas the chelicerae have until now, as a rule, been homologised with these latter organs.

A consideration of the accompanying table shows that the different regions of the body (the head, the thorax, and the abdomen) are not, in the various divisions of the Arthropoda, precisely homo-

TABLE TO FACILITATE A COMPARISON OF THE EXTREMITIES FOUND IN THE PRINCIPAL GROUPS OF THE ARTHROPODA.

Crustacea.	Xiphosura.	Arachnida.	Onychophora.	Myriopoda.		Hexapoda.
				Chilopoda.	Diplopoda.	
First antennae	—	—	Antennae *	Antennae	Antennae	Antennae
Second antennae	Chelicerae	Chelicerae	Jaws	—	—	—
Mandibles	First pair of legs	Pedipalps	Oral papillae	Mandibles	Mandibles	Mandibles
First maxillae	Second pair of legs	First pair of legs	First pair of legs	First pair of maxillae	Maxillae	First maxillae
Second maxillae	Third pair of legs	Second pair of legs	Second pair of legs	Second pair of maxillae	First pair of legs	Second maxillae (lower lip)
First pair of thoracic limbs	Fourth pair of legs	Third pair of legs	Third pair of legs	Maxillipedes	Second pair of legs	First pair of legs
Second pair of thoracic limbs	Fifth pair of legs	Fourth pair of legs	Fourth pair of legs	First pair of legs	Third pair of legs	Second pair of legs
Third pair of thoracic limbs	First pair of † abdominal limbs	First pair of ‡ abdominal limbs	Fifth pair of legs	Second pair of legs	Fourth pair of legs	Third pair of legs

* [Goodrich (No. II.) regards the antennae of *Peripatus* as belonging to the peristomial segment, while those of the Crustacea, Myriopoda, and Insecta he traces to the second post-oral segment.—Ed.]

† [According to Kishinouye and Packard (No. VII.), this would be the chilaria. See Vol. ii., p. 345, footnote.—Ed.]

‡ [This would be the transitory pre-genital segment of the Scorpion, according to Brauer, and a pre-genital segment which forms the waist in the Araneae (p. 57).—Ed.]

logous, for they are not formed of the same number of segments in all cases, nor are the same segments in all cases included in the similarly named body-region. The absence of a definite rule can be seen even in the Crustacea, in which the incorporation of thoracic limbs with the mouth-parts varies greatly in the different sub-divisions. Although we thus see that, in the great divisions of the Arthropoda also, the consecutive segments develop heteromorphously, we shall still be inclined to explain this fact by the requirements of the different functions, and shall not homologise the regions bearing similarly formed appendages. It will thus be quite possible to homologise the thoracic and abdominal appendages of one division with the cephalic and thoracic limbs of another, as in the table. That we are justified in such a course is shown, not only by the condition of the Crustacea already mentioned, but also of those Arthropods which we consider as the more highly developed, such as the Insecta. In the Hymenoptera, for instance, the first abdominal segment may join the thorax (segment médiaire),[*] and be so marked off from the abdomen as to appear much more like a thoracic than an abdominal segment. An omission, or rather a complete degeneration of single segments, such as must be assumed in the cases of the first antennae in the Arachnida and of the second antennae in the Myriopoda and Insecta (see the table), seems to be an exceptional occurrence. We are here leaving out of account the reductions undergone in many cases by the Arthropodan body (*e.g.*, in certain Crustacea, Arachnida, *Pentastomum*, and also many Insecta), and which often lead to a complete degeneration of the segmentation in different regions of the body or in the whole body, indeed, in the last case may even result in the disappearance of the division into body-regions. Such reductions may lead to the loss, not only of the segmentation, but also of the limbs (*Pentastomum*), a principal character of the Arthropoda being thus obliterated, but even in this case the development of larvae provided with extremities testifies to the Arthropodan nature of these forms.

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[*] Such a significance cannot any longer be ascribed to the segment médiaire of the Diptera (BRAUER, *Sitz. Akad. Wiss. Wien*, Bd. lxxxv., Abth. i., 1882), but there is evidently a close connection between the thorax and the abdomen in this order also.

LITERATURE.

Further information as to literature will be found at the ends of the chapters dealing with the different divisions of the Arthropoda.

1. ANONYMOUS. Bilden die Arthropoden eine natürliche Gruppe? *Kosmos.* Bd. xiii. 1883.
2. BEDDARD, F. E. On the possible origin of the Malpighian Tubules in the Arthropoda. *Ann. Mag. Nat. Hist.* (6). Vol. iv. 1889.
3. CLAUS, C. Ueber den feineren Bau des Medianauges der Crustaceen. *Anz. d. K. Akad. d. Wiss. zu Wien.* 1891. No. xii.
4. FERNALD, H. F. The Relationships of Arthropods. *Studies Biol. Lab. Johns Hopkins Univ. Baltimore.* Vol. iv. 1890.
5. GRENACHER, H. Untersuchungen über das Sehorgan der Arthropoden. *Göttingen,* 1879.
6. GRENACHER, H. Ueber die Augen einiger Myriopoden. *Archiv. f. Mikro. Anat.* Bd. xviii. 1880.
7. KINGSLEY, J. S. Is the group Arthropoda a valid one? *Americ. Naturalist.* Vol. xvii. 1883.
8. OUDEMANS, A. C. Ueber die Verwandtschaft und Classification der sog. Arthropoden. *Tijdschrift Nederlandsche Dierkundige Vereeniging* (2). Deel i. 1887.
9. SPENCER, B. On the Anatomy of Megascolides australis, the Giant Earth-worm of Gippsland. *Trans. Roy. Soc. Vict.* Vol. i. 1888.
10. WATASE, S. On the Morphology of the Compound Eyes of Arthropods. *Studies Biol. Lab. Johns Hopkins Univ. Baltimore.* Vol. iv. 1890.

APPENDIX TO LITERATURE.

I. ACLOQUE, A. Points de contact des Insectes avec les autres Arthropodes. *Naturaliste.* Tom. xix. 1897.

II. GOODRICH, E. S. On the relation of the Arthropod head to the Annelid prostomium. *Quart. Journ. Micro. Sci.* Vol. xli. 1898.

III. HANSEN, H. J. Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insekten. *Zool. Anz.* Jahrg. xvi. 1893.

IV. JAWOROWSKI, A. Zu meiner Extremitäten und Kiementheorie bei den Arthropoden. *Zool. Anz.* Jahrg. xx. 1897.

V. Kingsley, J. S. The classification of the Arthropoda. *Amer. Nat.* Vol. xxviii. 1894.

VI. Kowalevsky, A. Sur les organes excréteurs sur les Arthropodes. *Congrès Internat. Zool.* ii., 1. 1892.

VII. Packard, A. S. Further studies on the brain of Limulus polyphemus, with notes on its embryology. *Mem. Nat. Acad. Sci. Washington.* Vol. vi. 1893.

VIII. Patten, W. A basis for a theory of colour vision (comparison of the eyes of Acilius and Lycosa). *Amer. Nat.* Vol. xxxii. 1898.

IX. Viallanes, H. Études histologiques et organologiques sur les centres nerveux et les organes des sens des Animaux articulés. *Ann. Sci. Nat.* (7). Tom. xiii. 1892.

X. Wagner, J. Einige Betrachtungen über die Bildung der Keimblätter, der Dotterzellen und der Embryonalhüllen bei Arthropoden. *Biol. Centralbl.* Bd. xiv. 1894.

XI. Zograff, N. Sur l'origine et les parentes des Arthropodes, principalement des Arthropodes trachéates. *Congrès Internat. Zool.* ii., 1. 1892.

XII. Are the Arthropoda a Natural Group? Eleven papers by specialists on the different classes. *Nat. Sci.* Vol. x., pp. 97–117, 264–268. 1897.

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